UNIVERSIDAD COMPLUTENSE DE MADRID
FACULTAD DE CIENCIAS BIOLÓGICAS

TESIS DOCTORAL

Naturalización transcontinental de especies herbáceas en pastizales mediterráneos españoles y chilenos

MEMORIA PARA OPTAR AL GRADO DE DOCTORA
PRESENTADA POR

Irene Martín Forés

Directores

Miguel Ángel Casado
Belén Acosta-Gallo

Madrid, 2015

Naturalización transcontinental de especies herbáceas en pastizales mediterráneos españoles y chilenos

Irene Martín Forés

Memoria de Tesis Doctoral

Universidad Complutense de Madrid 2015

Naturalización transcontinental de especies herbáceas en pastizales mediterráneos españoles y chilenos

Irene Martín Forés

Memoria para optar al grado de Doctor

Universidad Complutense de Madrid 2015

Memoria presentada por Irene Martín Forés, licenciada en Ciencias Biológicas por la Universidad Complutense de Madrid, para optar al grado de Doctor.

Dirigida por el Dr. Miguel Ángel Casado y la Dra. Belén Acosta-Gallo, de la Universidad Complutense de Madrid.

El doctorando	Vº Bº del director	Vº Bº del director
Irene Martín Forés	Miguel Ángel Casado	Belén Acosta-Gallo

La presente Tesis Doctoral ha sido financiada por una beca de Formación del Profesorado Universitario (FPU, AP2009-0518) concedida por el Ministerio de Educación, Cultura y Deporte. El estudio presentado ha formado parte del proyecto nacional CGL2009-08718 financiado por el Ministerio de Ciencia e Innovación.

A Líam

Porque inundaste mi vida de luz desde el momento en que naciste y me miraste a los ojos, porque con una sonrisa haces que todos los problemas se desvanezcan y que la alegría invada todo mi ser, por lo que compartimos, por la complicidad, y por haber venido a este mundo a enseñarme tantas cosas. Te amo.

"A quien amas dale alas para volar, raíces para volver y motivos para quedarse"

Dalai Lama

"Give the ones you love wings to fly, roots to come back and reasons to stay"

Dalai Lama

AGRADECIMIENTOS

Sois tantos los que de un modo u otro habéis contribuido a la realización del presente estudio que me siento llena de gratitud y que me veo en la necesidad de empezar esta sección dando las gracias globalmente y excusándome por si, fruto del olvido, se me pasase algún nombre en el proceso de escritura.

En primer lugar me gustaría dar las gracias a mis directores de Tesis, Miguel Ángel Casado y Belén Acosta-Gallo, quienes, cada uno con su estilo y su forma de afrontar la dirección del presente estudio, siempre me han brindado un apoyo incondicional a lo largo de estos años de trabajo. A Miguel Ángel, por ser tan detallista y meticuloso, por aquellos momentos en los que comparte contigo una idea y te deja con esa profunda sensación de admiración. A Belén, por la cercanía, por ese debate existencial en el que la frontera entre lo ecológico, lo social y lo filosófico quedó derribada en nuestras cabezas mucho tiempo atrás… gracias por hacer que realmente haya disfrutado de mi final de Tesis. Gracias a ambos por enseñarme y compartir conmigo tanto, por la paciencia y guía a lo largo de todo este viaje, y por aceptar mi caótica vida y apoyarme no sólo en lo profesional, sino también en mis ilusiones y mis sueños.

Me gustaría además agradecer al resto del equipo de investigación, incluyendo a José Manuel de Miguel, Isabel Castro, Laura Sánchez-Jardón y Carlos Ovalle por su apoyo, y especialmente a Alejandro del Pozo, por su implicación, orientación y apoyo incondicional a lo largo de todo el proceso, y por brindarme la oportunidad de crecer a nivel personal y profesional durante mi estancia en Chile. Asimismo, me gustaría incluir aquí a Marta Avilés, quien recientemente se incorporó a nuestro equipo y contribuyó con su trabajo y su interminable sonrisa al presente estudio.

Quiero agradecer a la institución INIA-Cauquenes y a la Facultad de Agrónomos de la Universidad Politécnica de Madrid por las facilidades dispuestas para hacer parte del trabajo experimental del presente estudio. En especial a Teresa Aravena, Maria Elena Díaz y Teresa Moreno, por su apoyo técnico, y a Viviana Barahona, Irina Orieta Díaz y Daniel de la Torre por su apoyo logístico. Además, me gustaría reconocer aquí la ayuda proporcionada por Devayana Valero, Ricardo Prentice, Lilian Patricia Cáceres, y Alenjadra Lucía López quienes ayudaron en la obtención de parte de los datos para llevar a cabo el último capítulo de la presente Tesis.

Asimismo, quiero mostrar mi gratitud por el apoyo que recibí por parte de todo el equipo TERN, en la Universidad de Adelaida, durante mi estancia en Australia. En especial, me gustaría dar las gracias a Andrew Lowe, Stefan Caddy-Retalic, Eleanor Dormontt, Matthew J. Christmas, y Zdravko Baruch, por integrarme e incluirme en su equipo de trabajo, en sus ponencias y debates, así como en las actividades de ocio organizadas para favorecer la cohesión del grupo. Hicisteis que mi estancia allí marcase un antes y un después. Mención especial requiere Greg Guerin, quien siempre ha aportado a mi trabajo con sus sugerencias, consejos y correcciones, y siempre me ha ofrecido colaboraciones; gracias por hacer tanto por mí y creer en mí desde el principio.

Gracias a Berta Martín-López, por ser como un halo de luz que ilumina el camino de la investigación. La colaboración con ella y sus conversaciones y amistad siempre me ayudaron a no dudar de lo que espero en la ciencia, y a luchar por la transdisciplinariedad y los equipos cohesionados en los que realmente se coopera.

Gracias a mis compañeros, Sandra Magro, Katty Carrillo, Rocío de Torre, Daniela Gaspar, Adrián Escribano y Juan María Arenas, por las discusiones, por las sugerencias, los diferentes puntos de vista, las aportaciones y críticas constructivas.

Gracias a mis amigos, mi verdadera red… Mery, Álex, Euge, Óscar, Natxo, Cris, Kris, Mark, Esther, Nacho, Sonia, Jorge, Maikel, César, Alfon, Inma, Sabi, Nago, Marta, Mario, Laura, Luz, Mati, Arnau, Javi, Ángel, Steff… y un muy largo etcétera (soy muy afortunada de tener semejante compañía en mi vida!). Sois tantos los que siempre estáis ahí y sé que haga lo que haga vais a seguir queriéndome y vais a seguir construyendo las bases tan fuertes de cooperación y complicidad en las que se asienta mi vida.

Gracias a la Escuela Infantil 'La Libélula' y su encantador grupo de maestras. El último año y medio de trabajo ha sido mucho más fácil gracias a vosotras, contando siempre con vuestro apoyo, y sabiendo que mi hijo está en su segunda casa, en perfecta compañía y lleno de amor.

A Jerra, por su amistad y respeto por encima de cualquier cosa, por darme el mayor regalo de mi vida, y por apoyarme en los momentos difíciles de esta Tesis.

A mi tía Marta y mi prima Patricia, por ser tan cercanas como hermanas y ofrecerme siempre su ayuda.

A mis padres, Ramón y Amparo, y a mi hermana Inés, por el cariño, por la cercanía, por estar siempre dispuestos, por ofrecerme su ayuda en todo, por animarme a seguir en el camino hacia mis sueños. Por todo ello, gracias.

Y mi agradecimiento más especial, a Líam, mi hijo, el pequeño ángel que comparte mis momentos y mi 'ahora', el amor de mi vida… quien nació en medio del período de trabajo de la presente Tesis. Gracias por simplemente existir, por ser único, por irradiar tanta luz, por usar esa encantadora sonrisa para dar a mi vida todavía más alegría de la que ya tiene y por aportarme sin esfuerzo el impulso necesario para seguir adelante con todo manteniendo un pensamiento positivo.

ACKNOWLEDMENTS

There are so many people who, in some way or the other, have had contributed to the realization of the present study, that I feel full of gratitude and I am bound to globally thank everyone, and apologize in case I forgot any name in the writing process.

First of all, I would like to acknowledge my two supervisors, Miguel Ángel Casado and Belén Acosta Gallo, who, with their different style and way of face the supervision of the present study, have always supported me unconditionally. Thanks to Miguel Ángel for being so meticulous and for those moments when he shared with me some of his ideas and my main feeling was deep admiration. To Belén, for being so close, for our existential debate in which frontiers among ecology, society, and philosophy were knocked down long time ago… thanks for making me really enjoy the last step in the elaboration of the present Thesis. Thanks to both, for teaching me and sharing with me so much, for the patience and guidance throughout the whole journey this has being over the past five years, and for accept my chaotic life and support me, not only concerning my profession but also in my illusions and dreams.

I would like to thank the whole research team including José Manuel de Miguel, Isabel Castro, Laura Sánchez-Jardón, and Carlos Ovalle for their help, an especially to Alejandro del Pozo for his implication, guide, and unconditional support along the whole process, and for allowing me grow in a personal and professional way during my stay in Chile. Furthermore, I would like to also include here Marta Avilés, who recently joint our team, and contributed with her work and her endless smile to the present study.

Thanks to the whole INIA-Cauquenes institution and to the Faculty of Agronomy of the Polytechnic University of Madrid, for the facilities provided to carry out part of the experimental work. In particular to Teresa Aravena, Maria Elena Díaz, and Teresa Moreno, for their technical support, and to Viviana Barahona, Irina Orieta Díaz, and Daniel de la Torre for their logistical support. Moreover, I would like to recognize here the help provided by Devayana Valero, Ricardo Prentice, Lilian Patricia Cáceres, and Alejandra Lucía López who helped to get part of the data employed in the last chapter of this Thesis.

Likewise, I would like to show my gratitude to all the TERN team, at the University of Adelaide, for the way they treated me during my stay in Australia. Especially, I would like to thank Andrew Lowe, Stefan Caddy-Retalic, Eleanor Dormontt, Matthew J. Christmas, and Zdravko Baruch, for integrating and including me in their work-team, in their debates, as well as in the leisure activities organized to favor the group cohesion. You made that my stay there marked a turning point. Greg Guerin requires a special mention; he has always provided input, feedback, support, and advices to my work, and he has always offered me collaborations. Thanks for doing so much and for believing in me since the beginning.

Thanks to Berta Matín-López, for being like a halo of light that illuminates the path of researching. The collaboration and conversations with her and her friendship have always helped me to not have any doubt about what I expect from science, and to fight to accomplish transdisciplinarity and cohesive work-teams driven by cooperative processes.

Thanks to Sandra Magro, Katty Carrillo, Rocío de Torre, Daniela Gaspar, Adrián Escribano, and Juan María Arenas for the discussions, suggestions, different points of view and constructive criticism.

Thanks to my friends, my truly network… Mery, Álex, Euge, Óscar, Natxo, Cris, Kris, Mark, Esther, Nacho, Sonia, Jorge, Maikel, César, Alfon, Inma, Sabi, Nago, Marta, Mario, Laura, Luz, Mati, Arnau, Javi, Ángel, Steff… and a super long etcetera (I am very fortunate to have such a great company in my life!). There are so many of you who are always there, loving me no matter what I do, building the strong base of cooperation and complicity on which my life is settled.

Thanks to the International Nursery School 'La Libélula', and its lovely team of educators. The last year and a half has been easier by counting with your support, and by knowing that my kid is at 'his second home'.

To Jerra, for his friendship and respect above everything else, for giving me the most precious gift of my life, and supporting me in the hard times of this work.

To my aunt Marta, and my cousin Patricia, for being as close to me as sisters, and offer me always their help.

To my parents, Ramón and Amparo, and to my sister Inés, for the affection, the closeness, for being always willing to support, for offering me their help in everythig, for cheering me up to follow the way to my dreams. For all of them, thank you.

And the most special acknowledgment, to Liam, my son, the little angle who shares my moments, my 'now', the love of my life… who was born during the period of work of the present Thesis. Thanks for simply existing, for being unique, for glowing so much, and for using that charming smile to bring even more happiness to my life, and giving me the momentum I need to face everything maintaining always a positive thinking.

Imagine.
Imagine for a while.

No matter how long you keep quiet.
The light was definitively there.
Just have to catch it.
No matter what it takes.

Shades.
How understand them.
Shade, blue shade,
waves...
Between waves of chaos...

And meanwhile,
so unconsciously.
You loved your son.
Before you even hold him in your arms.
Before you even know him.

Life...
Reflections in blue...

Belén Acosta Gallo

I would like to thank Belén, for dedicating these beautiful words to me.

Me gustaría agradecer enormemente a Belén, por motivarme y sugerirme con estas bonitas letras que me ha dedicado.

CONTENTS

Naturalización transcontinental de especies herbáceas en pastizales mediterráneos españoles y chilenos

Transcontinental naturalization of herbaceous species in Spanish and Chilean Mediterranean grasslands

Resumen Abstract

"In one drop of water are found all the secrets of all the oceans; in one aspect of You are found all the aspects of existence."

— Kahlil Gibran

RESUMEN

La naturalización de plantas exóticas ha sido comúnmente considerada como una amenaza a la biodiversidad nativa. Pese al interés que suscita en la comunidad científica, algunos aspectos relacionados con el proceso de naturalización no están muy claros, incluyendo los factores que determinan el éxito en la colonización, cómo ocurre el ensamblaje de comunidades con las especies nativas y su evolución a lo largo del tiempo, y qué mecanismos favorecen la dispersión y subsiguiente expansión del área de distribución de las especies.

Actualmente, especies nativas y exóticas originarias de la cuenca mediterránea coexisten en los pastizales chilenos. En la región de Chile central, la cultura agraria introducida durante el colonialismo español determinó la entrada de numerosas especies desde España. El éxito del establecimiento y la persistencia (*i.e.* naturalización) de dichas exóticas en Chile pudo estar determinado tanto por las características del área de origen, como por factores medioambientales condicionantes de la llegada, supervivencia, establecimiento, ensamblaje en comunidades, reproducción, y finalmente expansión de estas especies en el área de destino.

El objetivo principal de este estudio consiste en dilucidar y comprender los mecanismos subyacentes en el proceso de naturalización transcontinental en Chile central. El trabajo se contempla a diferentes escalas espaciales (biogeográfica, comunidad y población), así como a lo largo de las diferentes fases del proceso de colonización (establecimiento, naturalización e invasión).

El estudio se ha llevado a cabo en sistemas agro-silvopastorales de las regiones mediterráneas de España y Chile, dehesas y espinales, respectivamente. Los datos empleados proceden de una exhaustiva revisión bibliográfica, de muestreos de campo llevados a cabo a lo largo de diferentes gradientes (latitudinal, de precipitación, sucesional y geomorfológico) y de diseños experimentales de siembra de poblaciones de *Leontodon taraxacoides, Hypochaeris glabra* y *Trifolium glomeratum* bajo condiciones uniformes en las áreas de origen y de destino.

En primer lugar, se estudió el contexto del área de trabajo mediante el estado de representación de la flora exótica en Chile. Nuestros resultados muestran que la mayor parte de las exóticas presentes en Chile son anuales procedentes de la cuenca mediterránea, siendo la proporción de las mismas mayor a escalas espaciales más detalladas (*i.e.* en los espinales). Las familias más representativas de estos sistemas son Poaceae, Asteraceae, y Fabaceae, y la especie más abundante *L. taraxacoides*. Los espinales y las dehesas son sistemas equivalentes en términos florísticos, aunque la riqueza de especies es mayor en España.

Para comprender los factores que condicionan el establecimiento, se compararon las condiciones del medio en las áreas de origen y destino. El clima actúa como principal predictor del potencial de establecimiento y naturalización de las especies seleccionando aquellas preadaptadas a las condiciones de destino. Las comunidades relacionadas con hábitats de influencia antrópica en el área de origen (por ejemplo, ruderales y asociadas a cultivos) actúan como principales donantes, aunque la importancia de las características del hábitat depende del clima de la región de destino, lo cual apunta a que la colonización es dependiente del contexto y la escala considerados.

El papel de los factores ambientales (bióticos y abióticos) como filtros de las especies en el proceso de naturalización fue evaluado a escala regional en espinales chilenos y dehesas españolas. La importancia de los filtros abióticos resultó ser mayor que la de los bióticos, aunque los primeros actúan de manera diferente

en ambas regiones. En España, las especies colonizadoras (aquellas que están naturalizadas en Chile) están ligeramente relacionadas con una combinación de propiedades climáticas y edáficas, mientras que en Chile el número de especies exóticas es altamente dependiente de las características climáticas, especialmente de la disponibilidad hídrica.

La organización espacial de la comunidad vegetal se estudió mediante la identificación de diferencias inter e intra-regionales en la co-ocurrencia de especies. Se encontró que las especies exóticas han desensamblado la comunidad chilena original, estando más segregadas espacialmente que las nativas, y más estructuradas en Chile que en España.

Los patrones de la dinámica temporal de la comunidad vegetal se estudiaron asociados al proceso de sucesión. Los resultados muestran que las especies exóticas y nativas juegan un papel complementario en la ontogenia de la comunidad a lo largo del tiempo mediante diferentes estrategias en la ocupación del espacio. Las especies exóticas, en su mayoría anuales tolerantes al pastoreo, se establecen desde el principio, mientras que las especies nativas, con estrategias de defensa frente al pastoreo, aumentan con el tiempo. Esto permite la coexistencia de ambos grupos de especies.

Los mecanismos adaptativos (diferenciación ecotípica y plasticidad fenotípica) en los que las poblaciones se basan para hacer frente a las nuevas condiciones ambientales y adaptarse a ellas se evaluaron en las tres especies seleccionadas. Poblaciones procedentes del territorio nativo y del exótico fueron sembradas en condiciones uniformes en Chile y España. La importancia relativa de dichos mecanismos de adaptación difiere según la especie considerada y la variable analizada. *L. taraxacoides* manifiesta principalmente plasticidad fenotípica para adaptarse al medio, mientras que *T. glomeratum* presenta una marcada diferenciación ecotípica, retrasando su desarrollo fenológico cuando procede de localidades más húmedas. Para las tres especies, las poblaciones exóticas (las que se originaron y sembraron en la región colonizada) muestran mayores tasas de supervivencia que las nativas.

Finalmente, la capacidad de dispersión fue evaluada mediante el estudio de la producción de semillas y los patrones de dimorfismo de aquenos de *L. taraxacoides* en Chile y en España. Los resultados muestran que esta especie combina diferenciación ecotípica y plasticidad fenotípica para aumentar el número de semillas producidas y la proporción de aquenos de dispersión anemócora en las poblaciones exóticas, a fin de incrementar su carácter invasor.

En oposición a la creencia tradicional de que la naturalización de exóticas supone un detrimento de la biodiversidad nativa, la coexistencia entre especies nativas y exóticas observada en los espinales chilenos durante todo el estudio parece pacífica. Ello, junto con la ausencia de competencia observada, sugiere que se están dando procesos de facilitación entre ambos tipos de especies. Nuestro estudio apoya que hay muchos procesos interconectados asociados a la naturalización transcontinental.

ABSTRACT

Naturalization of exotic plants has been commonly considered as a threat to native biodiversity, and scientific community has centered in its negative impacts instead of considering the possible benefits. Despite getting much scientific interest, some aspects related to the naturalization process are not well identified. Environmental factors determining the colonization success, how the assembly with native communities occurs and evolves along time, as well as mechanisms that favor spreading and expansion of the species' area of distribution are still little known.

Nowadays, native and annual exotics species originated in the Mediterranean Basin coexist in semi-natural grasslands of Chile. In central Chile many exotic species related to the agrarian culture were introduced during the colonialism by Spaniards. The success of establishment and persistence of those exotics in Chile (*i.e.* naturalization) was determined by the characteristics of the source area, as well as the environmental factors that condition the arrival, survival, establishment, assembling within communities, reproduction, and finally expansion in the recipient area.

The main aim of this study is to elucidate and understand the underlying mechanisms of the transcontinental naturalization process in central Chile. A multi-scale approach following a double connecting thread has been contemplated, considering different spatial scales (biogeographic, community, and population), as well as different phases of the colonization process (establishment, naturalization, and invasion).

The study was conducted in agro-silvopastoral systems of the Mediterranean regions of Spain and Chile, *dehesas* and *espinales*, respectively. Data employed came from extensive bibliographic revision, field sampling performed following different gradients (latitudinal, rainfall, successional, and geomorphological), and experimental observations conducted by growing *Leontodon taraxacoides*, *Hypochaeris glabra* and *Trifolium glomeratum* under common garden conditions in the source and recipient areas.

Firstly we evaluated the state of the art of the exotic flora present in Chile. Our results show that most of Chile's exotic plants are annuals from the Mediterranean Basin being the proportion greater at more detailed spatial scales (*i.e.* the greatest proportion is found in the *espinales*). The families more representative in these systems were Poaceae, Asteraceae, and Fabaceae, and the most abundant species *L. taraxacoides*. Agro-silvopastoral systems in Chile and Spain are equivalent in floristic terms, although species richness is greater in Spain.

To understand the factors conditioning the species establishment we compared environmental features between bioregions of source and recipient areas. Climate performs as the principal predictor of species establishment and naturalization potentiality, selecting species pre-adapted to the conditions in the recipient area. The communities related to habitats with greater anthropic influence in the source area (*e.g.* ruderal and arable lands) act as the main donors, although the importance of the habitat characteristics depends upon the climate in the recipient area. This points out that colonization is dependent on the context and the scale considered.

The role played by environmental factors (abiotic and biotic) through environmental filtering in the species naturalization was evaluated at regional scale, in Chilean *espinales* and Spanish *dehesas*. Results obtained show that abiotic filters are more important than biotic ones, although the first ones act differently in both regions. In

Spain, colonizer species (*i.e*. those that have become naturalized in Chile) are weakly related to a combination of soil and climate properties, whereas in Chile the number of exotic species is highly dependent on climate conditions, especially water availability.

Spatial organization of plant communities was study by identify inter and intra-regional differences in species co-occurrence. We found that exotic species have disassembled the original Chilean community, appearing more segregated than Chilean natives and being greater structured in Chile than in Spain.

Dynamic patterns of plant communities were assessed associated to a successional process. Results display that both species groups play a complementary role in community ontogeny along time by using different strategies in the occupation of the space. Exotic species are mainly grazing-tolerant annuals that get established from the beginning, whereas native species, with a grazing-defensive strategy, increase along time. This allows the coexistence of both species groups.

The adaptive mechanisms (ecotypic differentiation and phenotypic plasticity) on which populations rely on to face the new environmental conditions and get adapted in the non-native range were assessed in the three selected studies. Populations from the native and the exotic range were planted in common garden conditions in Chile and Spain. The relative importance of the adaptive mechanisms depends on the species considered and on the variable analyzed. *L. taraxacoides* relies mainly on phenotypic plasticity to get successfully adapted, while ecotypic differentiation appears to be important in *T. glomeratum*, which delays its phenological development when increased precipitation in the source area as a mechanism to maximize its investment in growth and biomass production. Exotic populations (those originated and grown in the non-native range) show greater survival rates than native ones in the three species.

Finally, the spreading capacity was assessed by studying seed output and achene dimorphism patterns of *L. taraxacoides* in Chile and Spain. Results reveal that this species combines ecotypic differentiation and phenotypic plasticity to increase the number of seeds produced as well as the proportion of achenes with anemochorous dispersion in populations from exotic origin in order to enhance its invasive ability.

In opposition to the traditional believe that exotics' naturalization always decreases native biodiversity or displaces it by exclusion, the coexistence between native and exotic species in Chilean *espinales* observed along the whole study seems to be pacific. This coexistence and the lack of evidences of competition suggest that facilitation processes are occurring between both types of species. Our findings support that many processes are interconnected with regard to the transcontinental naturalization process.

Naturalización transcontinental de especies herbáceas en pastizales mediterráneos españoles y chilenos

Transcontinental naturalization of herbaceous species in Spanish and Chilean Mediterranean grasslands

Introduction

"All things are delicately interconnected"

Jenny Holzer

ABOUT THE SYMBIOSIS BETWEEN NATURE AND HUMANS

The existing symbiosis between nature and human society (Naveh 2000) in the Earth system involves that to understand any ecological issue, a holistic approach that allows perceiving all parts in their full context is necessary (Palang et al. 2000). Human activity has given rise to a wide range of new planetary-scale forces (Steffen et al. 2004) that exert an increasing impact on the ecosphere affecting the different compartments it contains (Acosta-Gallo 2005), and creating cascades of repercussions on natural and socioeconomic systems (Schellnhuber 2005). The magnitude of that anthropic influence has increased so much that a new geological era has been recently recognized, the Anthropocene (Crutzen 2002).

The traditional blend of different anthropological cultures that has occurred for millennia usually involved trade, including the transport of merchandise, plants (mainly ornamental and forage), and domestic animals by humans along different regions worldwide, contributing to the generation of new environmental and socioeconomic scenarios (Le Houérou 1981; Hobbs 1998; Grenon and Batisse 1989). Associated to this trade, also flow of wild organisms around the planet (Elton 1958; Lodge et al. 2006) resulted favored; thus, species undertook a human-meditated overcoming of the biogeographic barriers to dispersal imposed by nature.

The above-described trend started in the Neolithic age, associated to the human displacements occurred in Southern Europe from the East to the West, which caused the introduction of archeophytes (*i.e.* exotic species that were introduced before 1500) in Western European territories such as the Iberian Peninsula. Later on, this trend has increased in three other phases; the first one occurred at the end of the Middle Ages (1500 AD), with the European rediscovery of the Americas, the birth of colonialism (Preston et al. 2004); the second one, associated with the Industrial Revolution (1800 AD) (Hulme 2009); and the last one during the last three decades, related to the rise in ease and efficiency of long-distance transport, income growth (Baier and Bergstrand 2001), and tourism (Hall 2015) which prompt the Globalization Era (Hulme 2009). As a result, species movement and worldwide interconnectedness have become more intensive, occurring across wider space and in shorter time than before (Pieterse 2015). Thus, humans' activities have introduced a new order of magnitude into distance dispersal (Cronk and Fuller 1995, and references therein) and species' areas of distribution (Levine and D'Antonio 2003; Perrings et al. 2005; Meyerson and Mooney 2007; Bradley et al. 2012).

The current scenario of anthropic impact on Earth altering ecosystem status is known as global change and is of mayor concern within an ecological framework. Basically it is a question of an unbalanced growth of human population in relation to the energy consumption by different societies (Margalef 1975) and the fact that human activities occurred at local or regional scale affects the global functioning of the planet (Pineda et al. 2014). It comprehends, among others, changes in carbon cycle (Acosta-Gallo 2005), climate (Vitousek 1994; IPCC 2014), land-use (Malone and Roederer 1984), and areas of species distributions (Vitousek et al. 1997). To face that, the UN convened the Millenium Ecosystem Assessment in 2000, with a view to evaluate the consequences of ecosystems' changes for human wellbeing and to improve conservation and sustainable use of these ecosystems (MA 2003, 2005; Montes et al. 2014).

As a result of the human-mediated transit of organisms (Paskoff and Manríquez 1999; Rouget et al. 2003; Dukes and Monney 2004; Schwartz et al. 2006) and habitat alteration, a redistribution of species on the Earth has taken place. This gives rise to economic and ecological damage (Vitousek et al. 1996, 1997; Pimentel et al. 1999, 2001, 2005; Mack et al. 2000; Sala et al. 2000) and a loss of cultural diversity. In this way, the subsequent biological invasions and biodiversity loss have important consequences at a variety of levels, affecting ecosystem structure (Vitousek et al. 1996), function

(Hooper et al. 2012), and services and human wellbeing (MA 2003; Corvalan et al. 2005; Díaz et al. 2006; Martín-López et al. 2009; Cardinale et al. 2012; Mace et al. 2012), being therefore considered as a major environmental and social problem and a focus of ecological research (Brock et al. 1997; Luken and Thieret 1997; Dukes and Mooney 1999; Higgins et al. 1999).

In the case of plants, the introduction of species in an exotic area took place as a result of the movement of specimens around the world with ornamental, gardening, agricultural and forestry purposes (Cronk and Fuller 1995, and references therein). Since agricultural practices were introduced in human cultures, whenever people moved, plants also did, either deliberately (domesticated crops) or accidentally (associated spread of weeds and ruderal species) (Cronk and Fuller 1995, and references therein). Due to their fast way of reproduction, their ability to withstand difficult environmental conditions through dormancy period in seed form, and the variety of ways of seed dispersal, exotic plants have been traditionally considered as a threat in the biological invasion context, with a greater number of invasive species than animals (Vitousek et al. 1996).

Notwithstanding the factors enabling establishment, one of the consequences associated to the colonization process that has been highlighted in previous reports is that alien species naturalization involves landscape and global floristic (taxonomic and phylogenetic) homogenization of regional floras at a biogeographical scale (Winter et al. 2009; Figueroa et al. 2011). Moreover, naturalization of alien plants has commonly been considered as a threat to native biodiversity, and most scientific studies have been centered in their negative impacts instead of considering the socio-ecological opportunities that the introduction of something new could bring. During the last decades numerous studies have highlighted the importance of control, monitoring and manage aliens introduced in new areas (Blossey 1999; Zavaleta et al. 2001; Pyšek and Richardson 2010; Barbier et al. 2013; Essl et al. 2015), and many conservation policies have been implemented to conserve the native flora and sometimes, although being controversial, eradicate alien invaders (Myers et al. 2000). As an example, the Strategic Plan for Biodiversity called for urgent action by the Parties to the Convention on Biological Diversity (CBD) to reduce the rate of biodiversity loss by 2020 (CBD 2014). To that end, they encountered the target of identifying, prioritizing, and managing invasion pathways by 2020 to prevent the introduction of invasive alien species (Hulme 2015).

Plant species that have been transported from one region to another are defined as non-native, exotic or alien to that new occupied region (Richardson et al. 2000). The resulting ecological consequence of the colonization process is a new and interesting case of community assembly (Dostál 2011; Davis et al. 2011; Sutherland et al. 2013), where species from different biogeographic origins —natives and aliens— coexist in the same community. Thus, the origin, composition, and assembly rules of these novel communities are of great interest (HilleRisLambers et al. 2012) to understand their functioning as well as serving as support to elucidate the drivers of vegetation change and predict the anthropic impacts on vegetation patterns (Chytrý et al. 2011).

Despite the fact that *a posteriori* actions of control and monitoring alien species have received most of the attention in scientific literature, knowing *a priori* mechanisms that allow and enhance the colonization process is key to globally deal with the current situation. Factors determining the 0) conditions of the source area, 1) arrival, 2) survival, 3) establishment, 4) organization within plant communities, 5) adaptation to local environmental conditions, 6) reproduction, and 7) following expansion condition the success of colonization (Richardson and Pyšek 2012). In this sense, the major processes involved in colonization process determining the distribution and abundance of alien plants have been identified (de Bello et al. 2005; Fine and Kembel 2011; Guerin et al. 2014; Rouget et al. 2015). Future areas of alien plants distribution will largely depend on the context within a regional species pool, which has a unique historical baggage associated with the environment and conditions

in which plant originated and grew (phase 0; Wiens and Donoghue 2004; HilleRisLambers et al. 2012; Lee et al. 2012; Hui et al. 2013). Afterwards, life-history traits and elements related to the introduction history determine species success of arriving to a new area (phase 1; casual aliens *sensu* Richardson et al. 2000). Later, this species pool must be able to survive (phases 2 and 3; established species *sensu* Richardson et al. 2000) and undergo environmental filtering. Alien plants must be able to survive in a particular abiotic environment (climatic, edaphic and land-use characteristics), given biotic interactions with the native vegetation community (Cornwell and Ackerly 2009; Kleyer et al. 2012), and self-perpetuate (Sax and Brown 2000) in the new area (phases 4, 5 and 6; naturalized species *sensu* Richardson et al. 2000). Additionally, ways of spreading and mechanisms related with dispersal, such as dissemination pathways, propagule pressure, residence time, or level of exposure to potentially invasible ecosystems (Wilson et al. 2007; Richardson et al. 2011, 2014) will determine the invasive ability of species (phase 7; invasive species *sensu* Richardson et al. 2000) (Fig. 1). Traits conferring adaptation and plasticity to the new environmental conditions and management practices are also critical during the whole process.

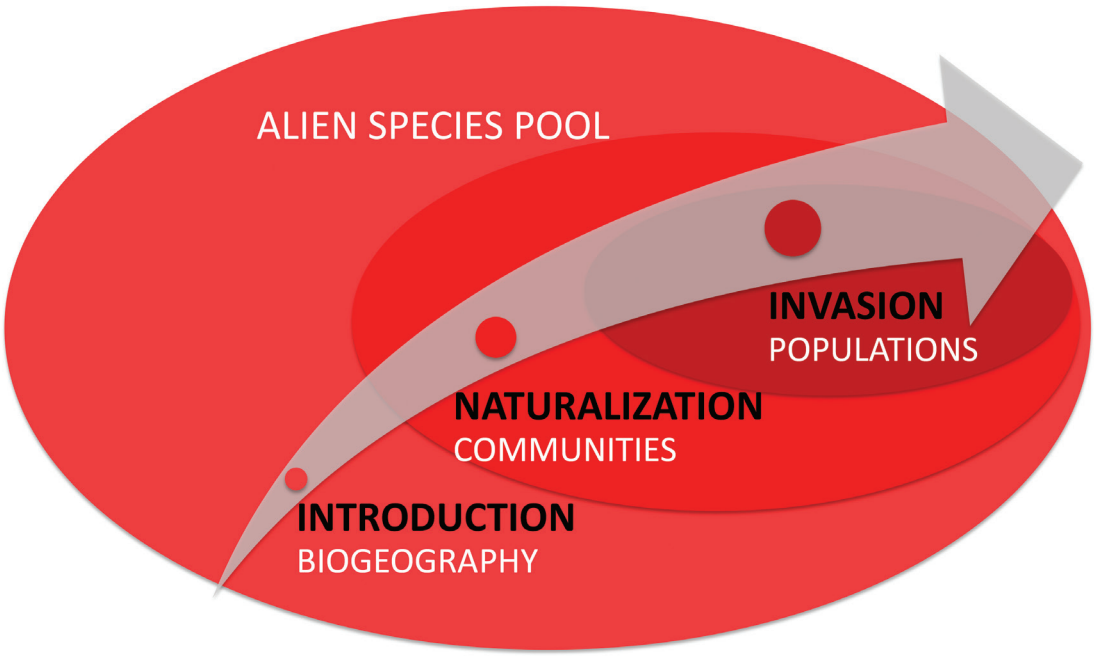

Fig. 1 A schematic representation of introduction-naturalization and invasion continuum and the scale of study (adapted from Richardson et al. 2000). Only a subgroup of introduced species becomes naturalized and, among them, only a fraction shows an invasive character

A special case: The Mediterranean basin and Mediterranean regions

The Mediterranean Basin was, around ten thousand years ago, one of the world cradles of agriculture and first human civilizations. During the Neolithic Era, the first forms of agriculture and human settlements came up in the territory known as Fertile Crescent, located in the Eastern Mediterranean, and comprising within the ancient territories of Mesopotamia and Near East. Back to that time, seven founder crops, including four cereals (wheat, einkorn, emmer wheat, and barley) and four pulses (lentil, pea, bitter vetch, and chickpea) were domesticated (Lev-Yadun et al. 2000); moreover, farming activities also started taking place, with the associated domestication of several livestock species, including mainly sheep, goats, cattle, and pigs (Zeder 2008). It took

about three millennia that the agrarian and farming culture got expanded throughout the whole Mediterranean Basin reaching the Iberian Peninsula (Estévez 1988; Boessneck and von den Driesch 1980; Fig. 2). Once agriculture and farming were integrated in humans' lives, food supply was under control and populations grew drastically, involving an increase in the dependence on and the intensification of agriculture (Brown et al. 2008).

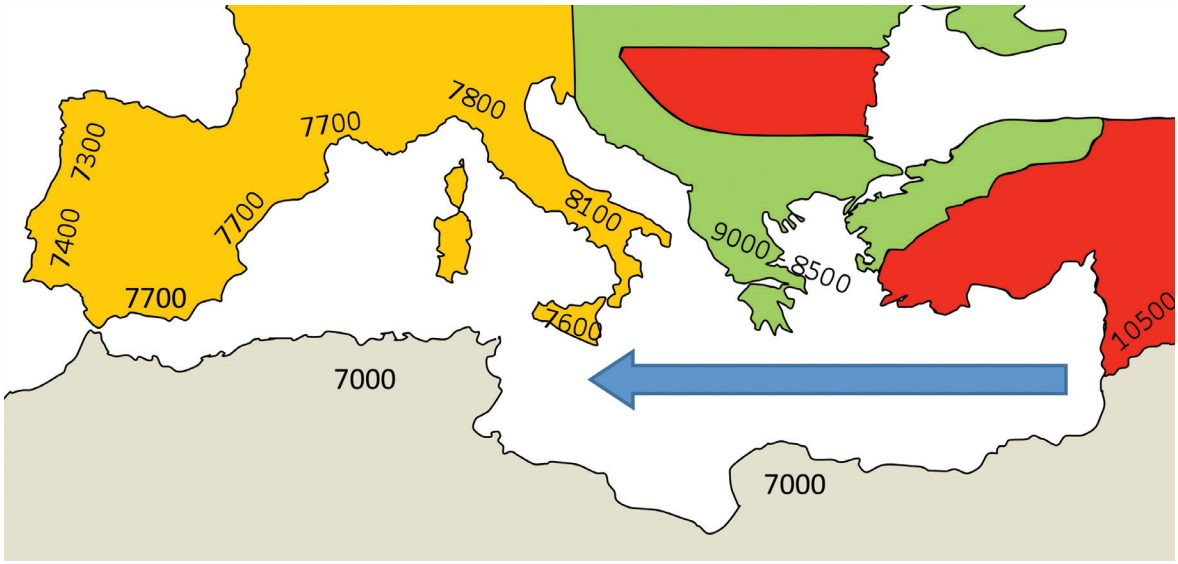

Fig. 2 An integrated model of the Neolithic expansion in the Mediterranean Basin. The location and approximate dates of colonist farming enclaves are shown by numbers (calibrated years before present). Red color represents the place settled by colonist farmers; yellow color indicateswhere indigenous foragers adopted elements of the Neolithic package and green color indicates areas of proposed integration of colonist farmers with indigenous foraging groups (modified from Zeder 2008)

Later on, a process of global exploration by Europeans known as colonialism took place at the end of the XV century, with consequences in human demography, agriculture expansion, and trade and industrial intensification. The expansion of the European colonial powers (remarkably Spain) radically increased the transport of living material. One major aim associated to colonialism was to exploit new economic crops for the empires. Particularly, the discovery of the New World by Spaniards coming from the Mediterranean Basin led to a great surge of plant exchange (Cronk and Fuller 1995, and references therein) among different Mediterranean-type regions. This phenomenon was specially marked when first female settlers established in the colonized lands (National Geographic Society, 1991). Because the morphologic, geographical, historical and societal characteristics of the Mediterranean Basin, especially those associated to demographic pressure and exploitation of land for agriculture and grazing, the territory presents since ancient times important patterns of land use change and anthropic effects on the environment leading to a cultural landscape (Pineda et al. 2002, Schmitz et al. 2005).

The Mediterranean climate is mainly characterized by mild wet winters and warm to hot, dry summers, and may occur on the west side of continents between about 30º and 40º latitude (Lionello et al. 2012). The summer drought period characteristic of the Mediterranean climate has become accentuated by the deforestation that has taken place around the Mediterranean during the last 2000 years, and the subsequent loss of plant evapotranspiration and evaporation from soils (Reale and Dirmeyer 2000; Reale and Shukla 2000; Dümenil-Gates and Liess 2001).

Mediterranean regions with the above-described climatic characteristics are located in five different continents of the planet, including the Mediterranean Basin, California, central Chile, South and South-Western Australia, and South Africa. Although sharing climatic patterns, they have had different biogeographical and environmental histories associated with the density of human populations as well as the time and intensity of the changes and land-use shifts that people have caused in the territory. Despite the Mediterranean biome is known for its diverse flora, including five of the biodiversity hotspots (Myers et al. 2000) comparable to tropical rainforest or coral reefs, it has been subjected to several impacts caused by humans but with different intensity and duration in each of the Mediterranean regions.

Among anthropic impacts of important concern are alteration of land use, habitat fragmentation caused by land-clearing and urbanization (Wade et al. 2003), climate change, alteration of fire regimes, and cross-introductions of alien species. In this sense, the millenary anthropic modification of the landscape occurred in the Mediterranean Basin, together with the human-mediated widespread alteration of biological patterns, species distributions and ecosystem land-uses have led to the formation of seminatural systems, cultural landscapes or anthropogenic biomes (anthromes *sensu* Rouget et al. 2015). In this socio-ecological-system, plants have co-evolved with people (Di Castri 1981; Perevolotsky and Seligman 1998) over a long time.

Similar cultural landscapes can also be observed in the other four Mediterranean regions worldwide, but the co-evolution of plants with humans has recently occurred, given that effective colonization times vary depending on the region considered (Fig. 3). Due to the fact that Mediterranean biomes are enough far away from each other to impede the natural flow of exotic species among them, aliens' spreading is expected to follow the cultural landscapes associated to main navigation routes from the period of colonialism onwards (Fig. 3; Fig. 4). Surprisingly, while in some Mediterranean-type ecosystems, a displacement of the native flora caused by alien invaders has occurred, this trend has barely been observed in others.

Fig. 3 Similarities among the five Mediterranean regions, the thickness of the connecting lines is proportional to the degree of similarity. The dates of European settlement of the four 'colonial' Mediterranean regions are given, as well as the distance between regions in nautical miles. The shorter distance for California-Mediterranean Basin is via the Panama Canal, the shorter distance for Australia-Mediterranean Basin is via the Suez Canal (modified from Fox 1990)

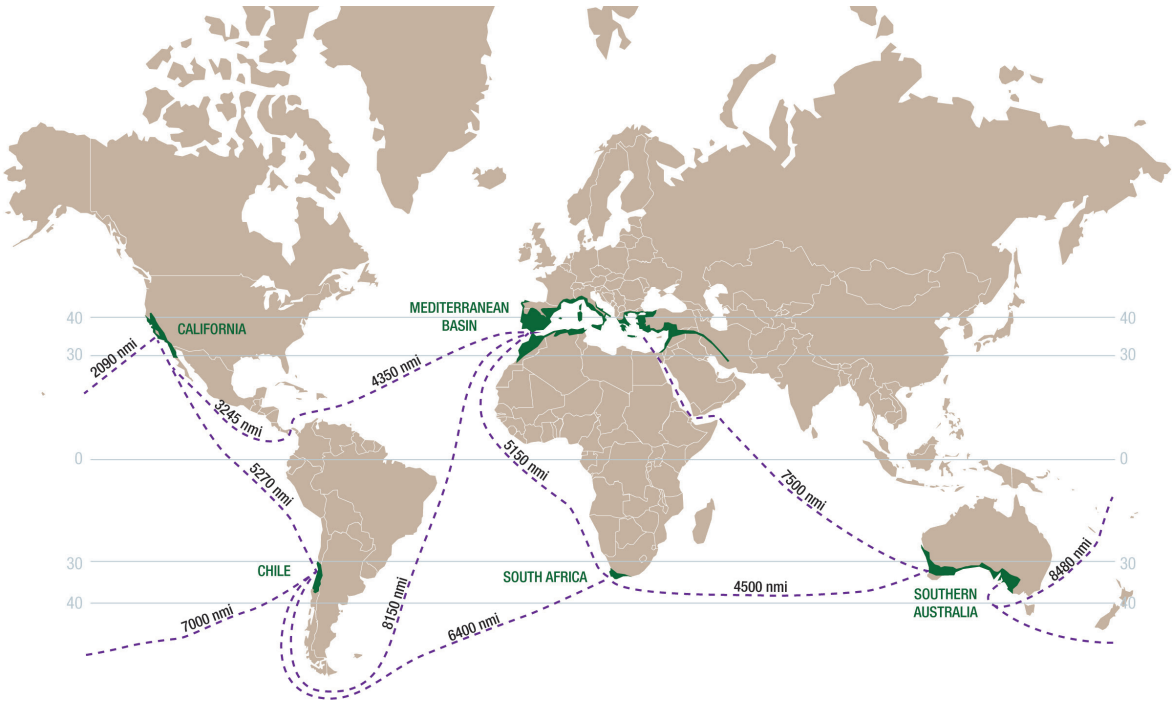

Fig. 4 Map of the world showing the five Mediterranean regions and the navigation routes among them. Distances between the regions are shown in nautical miles (modified from Fox 1990)

For all the above-exposed, Mediterranean-type ecosystems worldwide provide a great chance to compare and understand the mechanisms determining the success of species colonization of a given region (Kruger et al. 1989; Groves and Di Castri 1991). Nowadays, colonization process is considered a trending topic on which numerous research teams have worked (*e.g.* the teams led by HA Mooney, P Pyšek, A Pauchard, M Chytrý, DM Richardson, CM D'Antonio, and M Vilà, among others). Comparison of exotic floras between climatically similar regions constitutes a suitable tool allowing understanding the effects of landscape-scale changes associated with historical-cultural scenarios (Aschman and Bahre 1977; Kruger et al. 1989; Aschman 1991), and other aspects related with the naturalization process (Pauchard et al. 2004; Hierro et al. 2005). Among comparative studies of different Mediterranean-climate regions, those between Chile and California have been intensely analyzed (*e.g.* Parsons 1976; Arroyo et al. 1995a; Holmgren et al. 2000; Pauchard et al. 2004; Jiménez et al. 2008); similarly, comparisons between California and Spain (Leiva et al. 1997), or California and other geographic regions such as South Africa (Cowling and Campbell 1980) and Australia (Arroyo et al. 1995b). Despite the strong historical and socio-economic relationships between Chile and Spain, comparisons between the Mediterranean regions of these countries are scarce in scientific literature.

Considering the cultural, historical, and anthropological commonalities shared by both countries, Spain and Chile, and that those historical relationships between them favored the entry of exotic species coming from the Mediterranean Basin into Chile, it seems appropriate to contemplate the comparison between these two countries. Spaniards colonialism occurred in Chile during the XVI century and the implementation of European livestock and agricultural culture leaded to big direct (ploughing, cropping and grazing) and indirect (fire and deforestation employed as techniques for preparing the land for agriculture and livestock farming) changes, the extent of which are yet not well known (Turner et al. 1995). Particularly, in central Chile, sclerophyllous forests

were cleared and displaced by modified woodlands dominated by alien introduced species (Van de Wouw et al. 2011), and later those woodlands were opened for grazing and cropping, resulting transformed into grasslands mostly dominated by species from the Mediterranean Basin.

Associated to the Spaniards' arrival, alien species were introduced by exozoochory, coupled with merino sheep transported for wool trade, with hay for livestock fodder, and with wool and cereals (Castro et al. 2005). Several studies have associated the naturalization of those plants with processes of grazing by livestock (Holmgren et al. 2000; Pauchard and Alaback 2004; Del Pozo et al. 2006; HilleRisLambers et al. 2010). Thus, although Chilean and Spanish plant communities have undergone different process of invasion, previous reports highlighted the large number of species common to both regions (386, which is 64% of Chile's non-native flora; Pauchard et al. 2004).

Mediterranean regions of the Iberian Peninsula and central Chile also share agro-silvopastoral systems called *dehesas* and *espinales*, respectively (Fig. 5). They have a similar physiognomy (an anthropic savanna-like formation characterized by a continuous herbaceous layer with scattered trees), and land-use management (continuous extensive grazing with a low stocking rate in flatlands and rotation of grazing and cereal cropping in the better drained hillsides; Ovalle et al. 2005). Thus, natural and ancestral cultural factors based on silvopastoral activity converge in these scenarios (Ruiz Pérez 1986).

Fig. 5 Typical Spanish *dehesa* (left), and Chilean *espinal* landscape (right)

The origin of the *dehesa* dates back several centuries. It contains scattered trees of holm oak (*Quercus ilex* subsp. *ballota*) or cork oak (*Quercus suber*) within a herbaceous layer comprising mainly winter annuals (Joffre et al. 1999; Gea-Izquierdo et al. 2010) adapted to Mediterranean-type climate. *Dehesas* are characterized by a very high plant species richness (Pineda and Montalvo 1995), and cover about 3.5 million ha in South Western Spain (MAPA 2008) and about 0.7 million ha in Portugal (known as *montados*; Pereira et al. 2004). Savanna-like grasslands from the Iberian Peninsula are usually exploited by extensive livestock, especially for meat production (beef, lamb and pork), and breeding fighting bulls. Undoubtedly, they constitute an importance economic income, as well as a cultural patrimony, for being a reflection of the heritage of the cultural legacy since many centuries ago (Montoya 1983; Ruiz Pérez 1986; Pineda 1990; Pineda and Montalvo 1995; Pineda et al. 2002; Schmitz et al. 2005; Pineda and Acosta-Gallo 2012).

The *espinal* originated along the XVI century. It has dispersed trees of *Acacia caven* Mol. (the *espino*) within a herbaceous matrix comprising annual plants of Mediterranean origin (Olivares and Gastó 1971; Ovalle et al. 2005; del

Pozo et al. 2006). It supports a large rural population (350,000 people) and livestock (800,000 sheep and 250,000 cows) covering an area of 2 million ha in Chile's central zone (Ovalle et al., 1999) and a broad rainfall gradient from 200 to 1200 mm of annual precipitation. Like the *dehesa*, the *espinal* also presents high species diversity (Gulmon 1977; Del Pozo et al. 2006).

The *dehesa* represents the source and the *espinal* the recipient area for most of the exotic species of central Chile, and therefore they constitute an excellent scenario to study the process of colonization and naturalization of exotic species (Pauchard et al. 2004; Jiménez et al. 2008). The Chilean Mediterranean region, despite being a biodiversity hotspot (Ormazabal 1993), with high levels of regional and national endemism due to its biogeographic isolation (Myers et al. 2000), around the 18% of its flora (Arroyo and Cavieres 1997; Arroyo et al. 2000; Figueroa et al. 2004, 2011) is formed by alien species (507 exotics; Figueroa et al. 2011). Paradoxically, despite the percentage of alien species present and their early colonization, Chile is considered a region that has been less invaded or is in an earlier stage of invasion than other Mediterranean regions of the world (Arroyo et al. 2000; Figueroa et al. 2004; Castro and Jaksic 2008). Do to the similarities between the *dehesa* and *espinal* systems, points to consider that a higher percentage of alien species would have had the same potential to get naturalized in Chile, therefore, it is interesting to know the underlying mechanisms determining that some species arrive, establish, and become naturalized or even invasive and others do not.

Most of previous researches about colonization are focus on the regional scale and on the consequences of a single alien species. Moreover, usually they only study the naturalization process within the colonized region. Our approach constitutes a novelty considering the lack of studies that focus on plant communities and their relationship with ecological characteristics, as well as land-use and management, not only in the colonized area but also in the native range. Additionally, we assess plant community assembly including alien species, while classic studies (with few exceptions as Pyšek et al. 2005; Hui et al. 2013) used to focus only on native plants assembly within the community (Rouget et al. 2015).

Our international research team is formed by the Departments of Ecology of the Complutense University of Madrid and Autónoma University of Madrid, together with the Faculty of Agronomy at the Talca University, and the INIA Institution in Chile. The project called 'Naturalización transcontinental de especies herbáceas y organización espaciotemporal en pastizales mediterráneos'[1] has been recently developed by our team. Thanks to this, the role of this agroecosystems and the importance and curiosities of the novel communities created by the coexistence of native and exotic species can be assessed. The present study forms part of that project; it dedicates a considerable part of its efforts to elucidate and fully understand the underlying mechanisms of the transcontinental naturalization process. To face this general objective, a multi-scale approach has been contemplated.

1 Casado MA (Coord.) (2009) Naturalización transcontinental de especies herbáceas y organización espacio- temporal en pastizales mediterráneos. Spanish Ministry of Science and Innovation, reference CGL2009-08718

AIMS OF THE STUDY

The main aim of this study is to assess the ecological patterns and processes that have determined the alien species coming from the Mediterranean Basin got established, naturalized and subsequently organized within plant communities in the Mediterranean region of central Chile. There is a double connecting thread and continuity between different phases of the colonization process and different spatial-temporal scales associated with the barriers overcome in each phase (Fig. 6). Along the present study, the multi-approach followed goes from the more general processes —arrival and establishment— expressed at a biogeographical scale (Chapters 1 and 2), to those focused on naturalized plant communities and their relation with environmental filters (Chapter 3), as well as their organization in the space (Chapter 4) and time (Chapter 5). Finally, it focusses on finer spatial scales to study the adaptive mechanisms of different exotic species populations (Chapter 6), and the invasive ability of the most representative alien species in Chile (Chapter 7).

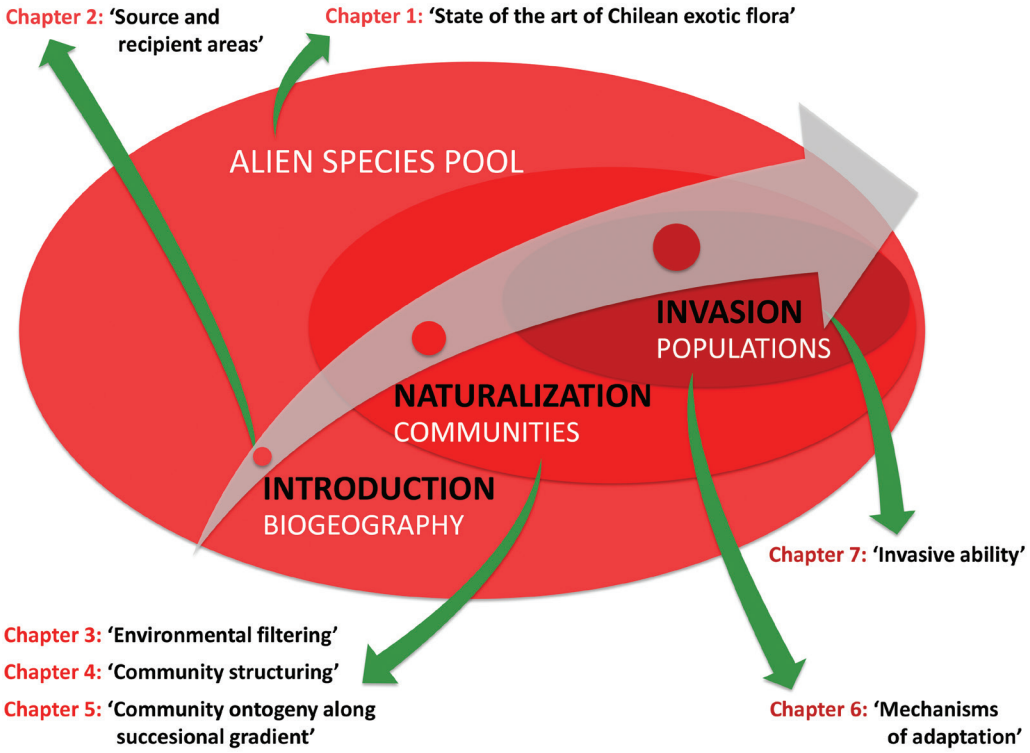

Fig. 6 The introduction-naturalization and invasion continuum and the scale of study at which phases of the colonization process are studied in each Chapter of the present study

First of all we focus on the state of the art of the alien flora present in Chile. Which alien species are already present in Chile? This constitutes a reflection of the arrival of exotic species to Chile and the subsequent establishment in the non-native range and it is addressed in the Chapter 1. This chapter consists on an evaluation of the current situation of the alien flora in Chile. The main aim is to analyze the relative significance of the biogeographic origin, lifecycle and representativeness of taxonomic families in Chile's alien flora in order to understand the context of the scenario that we want to compare to Spain. It is mainly descriptive, constituting the base of knowledge on which we proceed to state concrete hypotheses.

Once we know the Chilean naturalization context, we focus on understanding the arrival and the factors

conditioning the species establishment. As the state of the art reveals a possible preadaptation of the species that causes differential colonization depending on the climate and the biogeographic origin, we assess this phenomenon at a biogeographical scale in Chapter 2. It consists on a comparison of environmental features between bioregions of source —Iberian Peninsula— and recipient —Chile— areas following a latitudinal gradient. The main aim is to analyze the association of Chile's non-native herbaceous flora with the habitat characteristics of these species on the Iberian Peninsula.

We also evaluate environmental filtering at a regional scale focusing on plant communities which are the reflection of the species that have become naturalized. Thus, in Chapter 3, we assess the role of abiotic (climate and soil) and biotic factors on the process of naturalization of exotic species in central Chile, conducting a study along a rainfall gradient. Abiotic conditions can act in both, the source (by selecting those species with the highest potential to colonize other areas) and the recipient areas (by determining their success at establishing and spreading), but their effect might be different depending on the region of origin and evolutionary history of the species (natives or exotics). In the recipient area, success would be conditioned by the interactions with native Chilean species (biotic factors).

Another aspect that the state of the art reveals is that a different community organization might be occurring in the source and the recipient areas. Thus, in Chapter 4 we evaluate the community structuring in order to identify inter and intra-regional differences in the spatial organization (*i.e.* species co-occurence) of native and alien species in both, the native and the non-native ranges.

The study of the temporal organization of plant communities constitutes the main aim of Chapter 5. We assess the dynamic patterns of native and exotic species in the process of community ontogeny along a secondary successional gradient. Grasslands communities, mainly formed by annual herbaceous species are highly dynamic and studies assessing communities formed by a pool of native and exotic species together are scarce. Whether alien species always constituted a threat to native biodiversity, a detriment of native species would occur along succession due to the effect of alien species in the community.

Afterwards, we focus on the population scale, and evaluate the adaptive mechanisms on which populations of three species rely on to improve their success in colonization. The species of study are *Leontodon taraxacoides* (Vill.) Mérat. subsp. *longirostris* Finch and P.D. Sell, *Hypochaeris glabra* L., and *Trifolium glomeratum* L, native to Spain although naturalized and widely distributed in Chilean *espinales*. On the one hand, we evaluate differences in adaptive traits (*i.e.* plant survival, phenological development, and biomass and seed production) which allow elucidating the main adaptive strategies (phenotypic plasticity or ecotypic differentiation) employed by plants to successfully get adapted to the new environmental conditions imposed in their non-native range (Chapter 6).

Finally, in Chapter 7, we select *L. taraxacoides*, because of being the most abundant exotic species in Chile, and being considered as invasive (*sensu* Richardson et al. 2000). We study its invasive ability mainly focused on its spreading capacity, which might be determined by the seed output and the achene dimorphism patterns. What we want to evaluate is whether the propagule pressure and the capacity to spread vary depending on the origin and the environment of the population studied. If so, we would expect that the invasive ability appears enhanced by producing a larger number of seeds, and a higher proportion of central achenes within the capitulum, due to its anemochorous dispersal which confers them the ability to reach further areas.

Naturalización transcontinental de especies herbáceas en pastizales mediterráneos españoles y chilenos

Transcontinental naturalization of herbaceous species in Spanish and Chilean Mediterranean grasslands

Chapter 1 State of the art of the Chilean exotic flora

"History develops, art stands still"

Edward Morgan Forster

"Somewhere, something incredible is waiting to be known"

Carl Sagan

Adapted from: Martín-Forés I, Casado MA, Castro I, Ovalle C, del Pozo A, Acosta-Gallo B, Sánchez-Jardón L, de Miguel JM. 2012. Flora of the Mediterranean basin in the Chilean *espinales*: evidence of colonization. Pastos 42:135–158

INTRODUCTION

Historically, the transit of goods, domestic animals and people has favored the flow of wild organisms around the planet (Lodge et al. 2006), a fact that is often associated with the introduction of cultural systems, which have contributed to generate new environmental and socioeconomic scenarios (Le Houérou 1981; Hobbs 1998; Grenon and Batisse 1989). The current globalization process is increasing landscape changes and ecosystem disruptions by human disturbance and therefore facilitating the transit of organisms (Paskoff and Manríquez 1999; Rouget et al. 2003; Dukes and Monney 2004; Schwartz et al. 2006). These 'assisted dispersals' enable species to cross biogeographical boundaries that have previously limited their distributions. Species that have been transported from one region to another are defined as alien or exotic to that newly occupied region (Richardson et al. 2000). Most of these species fail to establish self-perpetuating populations, but some of them do succeed and become naturalized (Sax and Brown 2000). Regardless of the factors enabling establishment, the main consequence of this naturalization is that alien species significantly contribute to the global floristic (taxonomic and phylogenetic) homogenization of regional floras (Winter et al. 2009). Despite the fact that introduction of species increases diversity at short temporal and small spatial scales, in the medium and long term, interactions with native species can lead to extinctions (Pyšek and Richardson 2006). The net effect will depend upon the spatial and temporal scales considered and on the balance between naturalizations and extinctions (Sax et al. 2002). Nonetheless, the resulting ecological consequence is the coexistence of native species with exotic ones, quite often in the same community. The origin and composition of these novel communities are of great interest to understand their functioning and possible management.

Transcontinental naturalization in Chile's flora

Mediterranean-type ecosystems around the world offer a great chance to compare and understand the mechanisms determining the success of species introduced into a given region (Kruger et al. 1989; Groves and Di Castri 1991). The different regions presenting a Mediterranean climate have had different environmental histories associated with the density of human populations as well as the time and intensity of the changes that people have caused in the territory. In the Mediterranean Basin, anthropic modification of the landscape is millenary; however, rates of species extinction and naturalization are low in comparison with other Mediterranean regions (Greuter 1994). This fact is explained as a process of co-evolution of plants with people (Di Castri 1981). Conversely, other Mediterranean areas have undergone a rapid change following successive cultural colonialisms, some of these relatively recent, a fact that accounts for the current ecological conditions threatening the biodiversity of these areas (Underwood et al. 2009).

As occurs with other Mediterranean regions, Chile is recognized as a biodiversity hotspot (Ormazabal 1993), with high levels of regional and national endemism, possibly related with its biogeographic isolation (Myers et al. 2000). Its flora comprises 5364 native taxa, including species and subspecies (Marticorena and Quezada 1985; Marticorena and Rodriguez 1995, 2001) and between 552 and 723 alien species, depending on the author considered (Arroyo et al. 2000; Castro and Jaksic 2008). Paradoxically, despite the large amount of alien species present and their early colonization, Chile has been considered a region that has been less invaded or is in an earlier stage of invasion than other Mediterranean regions of the world (Arroyo et al. 2000; Figueroa et al. 2004; Castro and Jaksic 2008).

The arrival of exotic species to Chile started with the European colonization in the XVI century (Arroyo et al. 2000; Figueroa et al. 2004), which marked the first deliberate introduction of animals and plants (Montenegro et al. 1991; Jaksic 1998). The rate of species entry in these early days is unknown, since the initial systematic botanic

descriptions of flora date from the XVIII century and were performed by botanists who were more interested in describing the native species than on the exotic ones (Gay 1845-1854; Reiche 1896-1911). By the end of the XVIII century, numerous exotic species had become naturalized in Chile (Figueroa et al. 2004), such as *Cardamine hirsuta* L., *Medicago polymorpha* L., *Spartium junceum* L. and *Bromus hordeaceus* L. (Castro et al. 2005). Although this species introduction has not been consistent over time, a rate of two to three species per year is estimated, which is lower than the four to six species recorded for other Mediterranean regions (Groves 1991; Kloot 1991; Rejmánek et al. 1991; Wu et al. 2003).

Processes and mechanisms in species introduction

Changes in land use constitute the main factor determining processes of colonization and naturalization of plant species (Le Houérou 1991; Huston 1994; Holmgrem et al. 2000). Among the most influential factors, deforestation, fires and particularly agricultural practices have been highlighted (Le Houérou 1991; Cowling et al. 1996; Williamson 1996; Hobbs 1998). With regard to deforestation, although Chile still has one of the biggest areas of temperate forest in South America (Donoso 1993), much of it has been deforested for pastures or croplands. This process started in the XVI century, although the main boom was during the middle of the XX century, with the expansion and intensification of wheat crops (Echeverría et al. 2006) and the spread of forestry plantations. In relation to fire, unlike other Mediterranean climate areas, fire has not constituted a factor of natural disturbance in Chile (Muñoz and Fuentes 1989; Gómez-González and Cavieres 2009), a fact that accounts of the absence of specific adaptations in native species. Although there is evidence of fires of human origin in earliest settlements in the region, around 14,000 years ago, these were not significant until the arrival of the Spanish (Aronson et al. 1998; Aravena et al. 2003; Villa-Martínez et al. 2003). Subsequently, fires became more frequent and intense, and currently about 5,000 ha of native shrubland are burnt each year, the vast majority of these fires being intentional (Gómez-González and Cavieres 2009). It has been suggested that plant communities under novel fire regimes are more susceptible to invasion than those under a natural (historical) fire regime (Trabaud 1991; D'Antonio 2000). However, different studies that have analyzed the effects of fire upon native and non-native Chilean flora appear to indicate that fire is not a relevant factor with regard to favoring non-native species (Keeley and Johnson 1977; Holmgrem et al. 2000; Gómez-González et al. 2010). Fire does, however, constitute a notable advantage for the establishment of annual plants, which are poorly represented in Chile's native flora (Arroyo et al. 1995).

The implementation of European agricultural culture in the XVI century leaded to big changes in land uses and landscapes in Chile, the extent of which are yet not well known (Turner et al. 1995). The effects of agriculture have been both direct (plowing, cropping and grazing) and indirect (fire and deforestation, employed as techniques for preparing the land for agriculture and livestock farming). Livestock was introduced into Chile, perhaps at the same time as the colonization by Europeans. Other herbivores, however, such as rabbits and hares, were brought more recently, in the XIX century (Jaksic and Soriger 1981). Several studies have associated the naturalization of exotic plant species with grazing by both livestock (Holmgren et al. 2000; Pauchard and Alaback 2004; Del Pozo et al. 2006; HilleRisLambers et al. 2010) and rabbits (Sáiz and Ojeda 1988; Holmgren et al. 2000; Holmgren 2002). The effect of grazing on native or non-native species has been characterized using morphofunctional plant traits, revealing differences in their response. For instance, grazing appears to favor some exotic creeping species, such as *Erodium cicutarium* (L.) L'Hér. and some leguminous species, in detriment to the upright ones, the latter more closely associated with native species (Holmgren et al. 2000). Grazing also favors substitution of native hemicryptophytes by both native and non-native annuals, capable of resisting periods of drought stress as seeds.

Many exotic plants were also introduced associated with crops, and became widely distributed as a result of the importance of agriculture in the country (Castro et al. 2005). Crop fields, particularly along their succession stages following abandonment, constitute the ecosystems presenting the highest values for richness and cover of non-native plants in Chile (Figueroa et al. 2011). Since colonization the introduction process has continued, although with different rates along time. Thus, Aronson et al. (1998) highlight an initial wave of exotic species from 1880 to 1920 associated with transformation of the landscape. Fuentes et al. (2008) recognize an initial phase (1910-1940) associated with intense development of agriculture (Cariola and Sunkel 1982), as well as a second phase (1980-2000) related with a sharp increase in the mechanization of farms and forest plantations at large scale. Matthei (1995) describes a sustained increase in the naturalization of exotic species from 1894 to 1934 associated with wheat imported from other countries.

Although many species were accidentally introduced into Chile (Arroyo et al. 2000), many were taken for agricultural, medicinal, culinary and, more recently, ornamental purposes. Since the arrival of the Spanish, species were introduced associated with hay for livestock fodder and with wool and cereals. Endozoochory likely constitutes the most frequent mechanism of effective seed dispersal. However, during transit from Spain to Chile, exozoochory was probably the most effective mean of dispersal, given the difference in time between the transoceanic voyage and the time required for seeds to pass through an animal's digestive tract (generally less than one week; Malo and Suárez 1997). Europe was not the only center of introduction of non-native species to Chile. During the Gold Rush, in the middle of the XIX century, there was intense wheat trading with California (Davis 1894), a fact which mobilized other species, together with grain and straw, in both directions (Le Houérou 1991, Jiménez et al. 2008), especially from Chile to California.

Comparative studies of transcontinental naturalization

Comparison of non-native floras between climatically similar regions constitutes a very useful tool for understanding aspects associated with the species naturalization process (Pauchard et al. 2004; Hierro et al. 2005). It can help us to understand the effects of changes in the landscape associated with historical or cultural scenarios upon the naturalization process (Kruger et al. 1989; Aschman, 1991). Among comparative studies of different regions with Mediterranean climates, those between Chile and California have been intensely analyzed (*e.g.* Parsons 1976; Arroyo et al. 1995; Holmgren et al. 2000; Pauchard et al. 2004; Jiménez et al. 2008). These researches highlight the large number of species common to both regions (386, which is 64% of Chile's non-native flora; Pauchard et al. 2004), as well as the fact that their communities are undergoing different process of invasion with similar consequences of floristic homogenization (Figueroa et al. 2011). However, to date there have been no comparative studies between Chile and Spain, despite their climatic and geomorphological similarity, the historical relationships that favored the entry of species into Chile and the large number of species common to both countries. Many of these naturalized species are associated with the *espinal*, an agroecosystem presenting a management system and structure similar to those of the Spanish *dehesa* (Ovalle and Avendaño 1987; Ovalle et al. 1990). However, as these agricultural systems are similar in both countries, we are not fully aware of the mechanisms underlying the arrival of determined species and the subsequent naturalization and spread thereof.

The aim of this paper is analyze the relative significance of the biogeographic origin, lifecycle and representativeness of taxonomic families in Chile's non-native flora. We considered three scales of analysis: national, regional (the central zone presenting a Mediterranean climate) and community (the *espinales* within the central zones). In the third case, we also conducted a comparative study with Mediterranean grasslands from

the Iberian Peninsula in order to identify the degree of similarity in the floristic composition of communities with comparable ecological and agronomic characteristics.

MATERIAL AND METHODS

Study area

The *espinal* is an anthropic savannoid formation characterized by dispersed trees of *Acacia caven* Mol. (the *espino*) within a herbaceous matrix comprising mainly annual plants of Mediterranean origin (Olivares and Gastó 1971; Ovalle et al. 2005; del Pozo et al. 2006). It supports a rural population of approximately 350,000 people, as well as the largest Chilean livestock: 800,000 sheep and 250,000 cows. It covers an area of two million hectares in Chile's central zone, ranging along the Central Valley and the western slopes of the Coastal mountain range (Ovalle et al. 1999). It currently occupies mainly the dryland sectors (Fig. 7), from the river Petorca (32° S), bordering on the arid Mediterranean region, to the river Laja (37° S), bordering on the perhumid region (Fuenzalida and Pisano 1965; Di Castri 1968; Quintanilla 1981; Rodríguez et al. 1983). Further north, in the arid and perarid regions, some *espinales* can be found, preferentially located in valley bottoms (Follman and Matte 1963; Rodríguez et al. 1983). Their distribution is associated with Mediterranean-climate areas, albeit with very variable annual rainfall, from 160-200 mm at its northern limit and up to 1000-1200 mm at the southern one. It presents high species diversity (Gulmon 1977; Solbrig et al. 2002; Del Pozo et al. 2002) and to date, 215 species have been identified only in the Cauquenes region (Ovalle et al. 1987). It originated through changes in land uses after the Spanish conquest; the native sclerophyllous forest was cleared in order to open up land for agriculture and livestock farming, which favored gradual invasion by the exotic species A. *caven* (Gulmon 1977; Armesto and Pickett 1985; Ovalle et al. 1990), possibly from South America's Gran Chaco (Holmgren 2002).

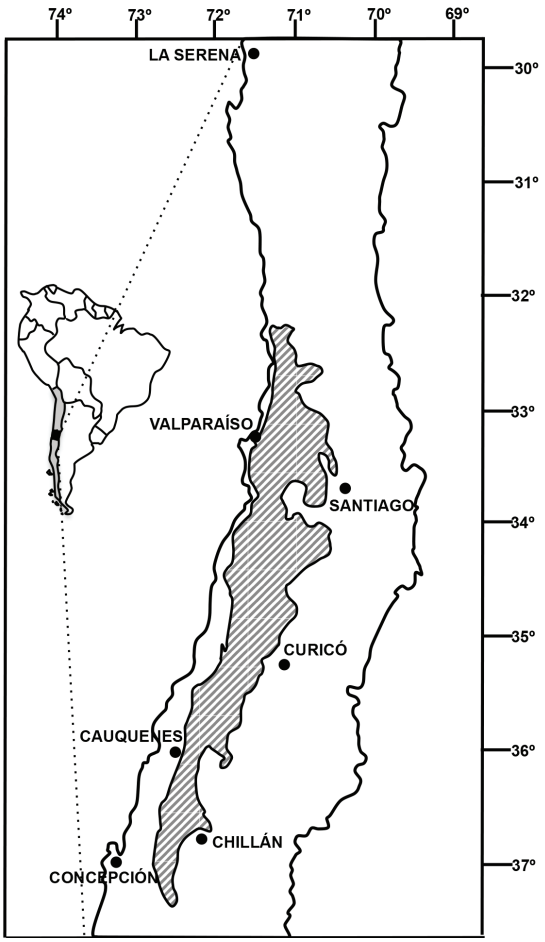

Fig. 7 Location of Chile (in grey) in South America and enlargement of the central zone. The shaded area represents the main distribution areas of *espinal* (modified from Ovalle et al. 1999)

The *espinal* is an agrosilvopastoral system presenting much similarity with the Spanish *dehesas* and Portuguese *montados*. It has traditionally been based upon two models of management: continuous extensive grazing in flatlands, occasionally inundated during winter, and rotation of grazing and cereal cropping in the better drained hillsides (Ovalle et al. 2005). In the latter case, the *espino* is periodically cut down for firewood and charcoal. The land is subsequently ploughed for sowing cereal crops. After one or two years' harvest, depending upon the fertility of the soil, the land is abandoned and colonized by herbaceous

species, while shoots grow from the stump of the *espino*. In this phase, the land is used for extensive grazing with a low stocking rate of approximately one sheep/ha (Del Pozo et al. 2006). The grazing period prior to the following cropping cycle is variable, from three to 40 years, depending on the fertility of the soil.

The *espinal* is currently more degraded than in past times. In the first place, an increasingly greater area of the *espinales* in the Central Valley is being replaced by intensive irrigation agriculture. Furthermore, many owners have abandoned their traditional farming activities for forest plantations (approximately 80,000 ha/year), mainly of *Pinus radiata* D. Don or *Eucalyptus globulus* Labill. Finally, the territory still maintaining functional *espinales* has usually low fertility and soil erosion, leading to low agricultural production. At present, 40% of the area is occupied by *espinales* with very little tree cover (<25%) and 4% is dominated by romerillo (*Baccharis linearis* (Ruiz and Pav.) Pers.), which indicates a situation of degradation and abandonment. Under these circumstances, the cereal-pasture rotation system is in decline and limited to small areas, almost exclusively for people's own consumption.

Methodology

For our research we developed a database containing all non-native species found in Chile. We used the catalogue of Chilean flora by Marticorena and Quezada (1985, 1987), along with information provided by the *Laboratorio de Invasiones Biológicas de la Universidad de Concepción* (http://www.lib.udec.cl/database.html). This list was complemented with an extensive bibliographic revision incorporating some exotic species recently cited in the country. Each species was characterized by assigning its taxonomic family, area of origin, life cycle and distribution range within Chile. To assign the area of origin and life cycle we used different regional floras, fundamentally *Flora Ibérica* (Castroviejo et al. 1986-2010), *Flora Europaea* (Tutin et al. 1964-80) and *Flora del Cono Sur* (Zuloaga et al. 2008). As regions of origin we considered the four big continents: Eurasia, Africa, America and Australasia. Apart from these four large regions we considered independently the Mediterranean Basin (SE, S and SW of Europe, N Africa and SW Asia), given the non-native typology of species present in Chile. Species present in more than one continent were classified as Cosmopolitan. As for the life cycle trait, we classified them into three groups: annual, perennial herbaceous and woody species. Finally, for the distribution range within Chile we took the 15 administrative regions as units (from the Tarapacá Region in the far north to the Magallanes Region at the southern limit), excluding the species present only on the islands belonging to Chile (Easter Island and the Juan Fernández archipelago). We obtained these data mainly from Castro et al. (2005), Martincorena (http://www.lib.udec.cl/database.html) and Zuloaga et al. (2008). We considered the set of non-native species present throughout the country, as well as those distributed only in the central zone (from the Coquimbo region in the north to the Bío-Bío Region in the south; Fig. 7).

In order to complement our database of non-native species, in 2010 we conducted field samplings, both in Chilean *espinales* and in Spanish Mediterranean grasslands. In each country we selected 15 sites and in each one we chose two 10 x 10 m plots in which we randomly distributed six 50 x 50 cm quadrats. In each quadrat we recorded the presence of all plant species. Each species was assigned a value of frequency according to the number of sites in which it was recorded in each country. The 30 sites selected presented similar lithological characteristics (acidic materials associated with igneous or metamorphic rocks), geomorphological ones (undulating topography) and those relating to use history (management for extensive livestock farming). In the case of Chile the 15 sites were distributed within the Mediterranean region, over more than 600 km, from 32º 31' 35'' to 37º 00' 10'' S latitude. In the case of Spain the 15 sites were distributed within the center-western

areas (Extremadura, N Andalucía and W Castilla-La Mancha, from 40º 14' 45'' to 37º 51' 40'' N latitude). For all species of European origin, we standardized the nomenclature in accordance with *Flora Ibérica* (Castroviejo et al. 1986-2010), and in the case of families as yet unpublished in this study, with *Flora Europaea* (Tutin et al. 1964-80).

RESULTS

The list of Chile's non-native flora comprises 773 species or subspecies, which, following exclusion of spurious citations, was reduced to 698 taxa (548 in the central zone and 75 in the *espinales*), 50 of which are woody species and the rest herbaceous ones. This large set of species is distributed into 72 families, of which the best represented ones at country scale are Poaceae (19.8% of species), Asteraceae (13.9%) and Fabaceae (10.2%). This distribution of species into families is very similar when the Chile's central zone was exclusively considered (Fig. 8). However, the spectrum of families present in the flora of the *espinales* is very different, and is characterized by a higher proportion of Poaceae, Caryophylaceae, Rubiaceae, Rosaceae and Geraniaceae, and a decrease in the proportion of Brassicaceae.

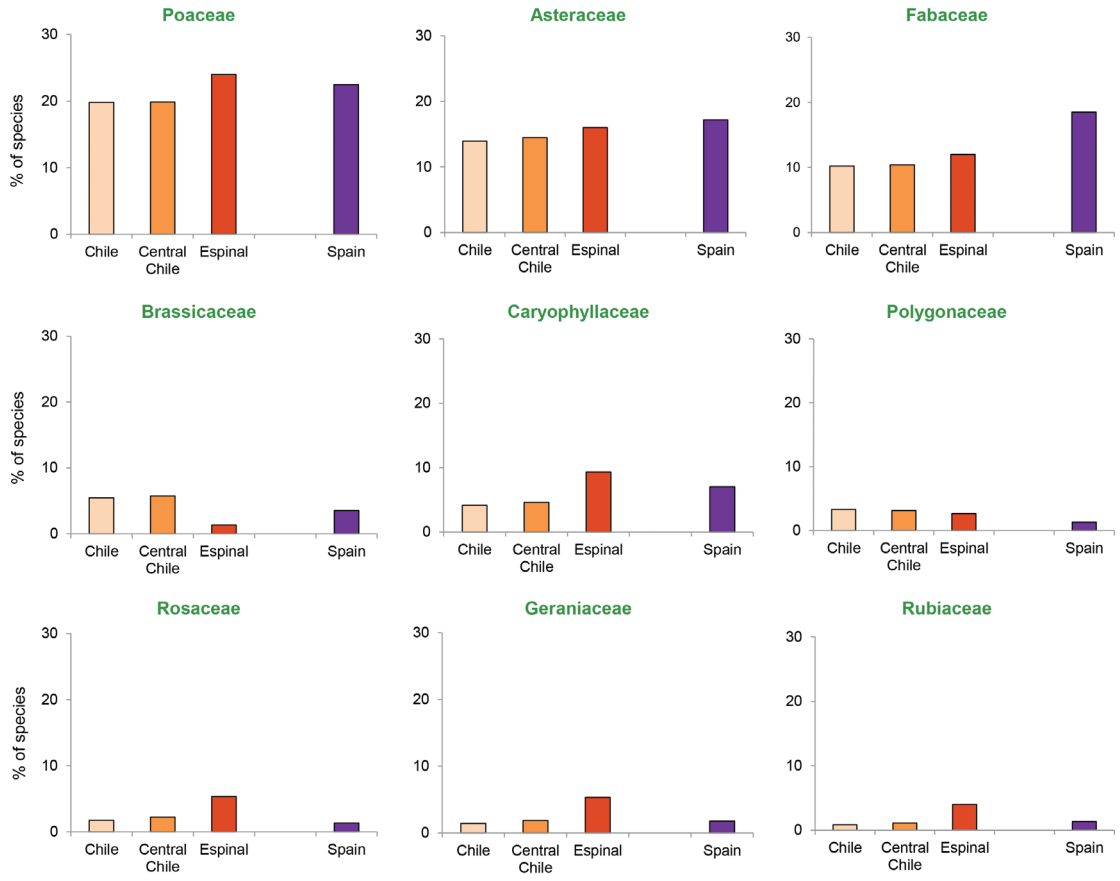

Fig. 8 Frequency histograms of the distribution of non-native species according to taxonomic families. Only the nine most represented families are shown. Each histogram shows the frequency calculated at country scale (light orange bars; n= 698 species), of Chile's central zone (medium orange bars; n = 547 species) and of the *espinales* (dark orange bars; n= 75 species). In the case of Spanish grasslands (purple bars) frequency was calculated with the total number of species found in the field samplings (n = 229 species)

This distribution into families of the *espinales* is relatively similar to that seen in Spanish grasslands, except for the fact that Spain presents more Fabaceae (18.5% vs 12%) and Brassicaceae (3.5% vs 1.3%), and the *espinales* more Caryophylaceae (9.3% vs 7.1%), Rubiaceae (4% vs 1.3%), Rosaceae (5.3 vs 1.3%) and Geraniaceae (5.3% vs 1.8%).

With regard to the area of origin of Chile's non-native species, at the scale both of country and of the central zone, species of Eurasian origin (39.7%) dominate and, to a lesser degree, those of Mediterranean origin (28.4%) (Fig. 9). However, when only the flora of the *espinales* is considered, the species from the Mediterranean Basin increase to 49.3% and those of Eurasian origin to 48%, thus Eurasia in the broader sense constitutes the area of origin of 97.3% of non-native species. This tendency is maintained in Spanish grasslands, with values of 97.8% for species from Eurasia (72.1 and 25.7% for species of Mediterranean and Eurasian origin, respectively).

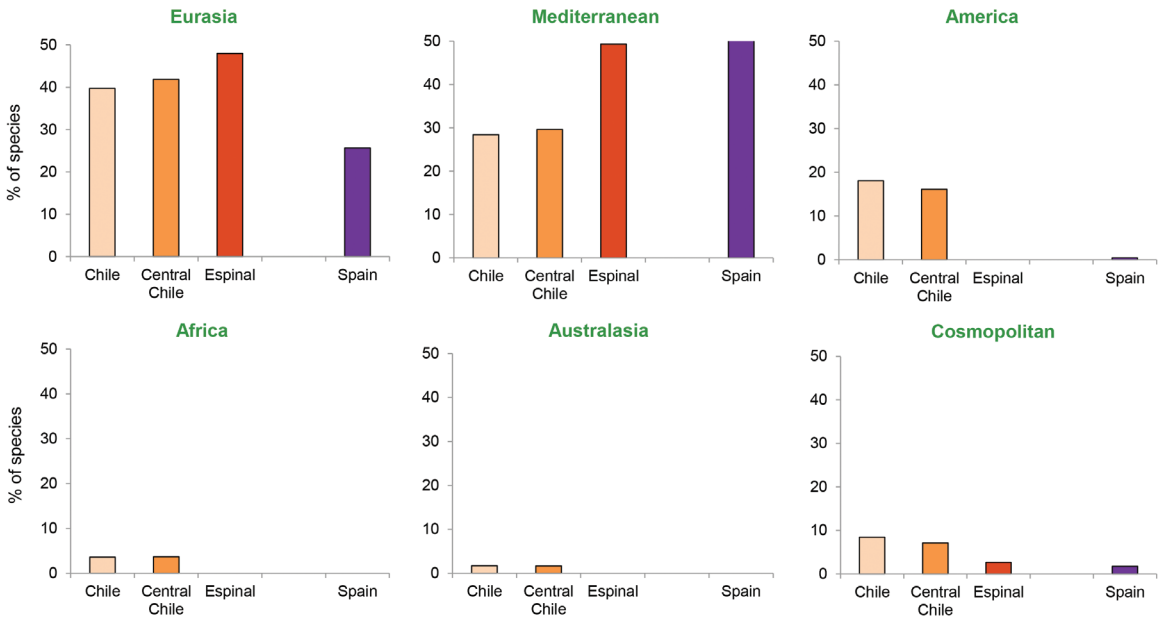

Fig. 9 Frequency histograms of the distribution of non-native species according to the region of origin. Each histogram shows the frequency calculated at country scale (light orange bars; n = 698 species), of Chile's central zone (medium orange bars; n = 547 species) and of the *espinales* (dark orange bars; n = 75 species). In the case of Spanish grasslands (purple bars) frequency was calculated with the total number of species found in the field samplings (n = 229 species)

Both in Chile as a whole and in the central zone, the vast majority of non-native species are herbaceous, both annual (55.8%) and perennial (37%) (Fig. 10). This trend is accentuated in the *espinales*, where none exotic woody species have been found and annual plants represent 84%, a value very similar to the 81.2% of annual species found in Spanish grasslands. Life cycle (annual, herbaceous perennial and woody) is not independent from the area of origin of the non-native species (table of contingency between areas of origin x life cycle, χ^2=169.18, $p < 0.001$): among the species of African and American origin there are significantly more woody and perennial herbaceous plants than expected at random; among those of Mediterranean origin there are significantly more annual species; and among those of Australian origin there are significantly more woody species.

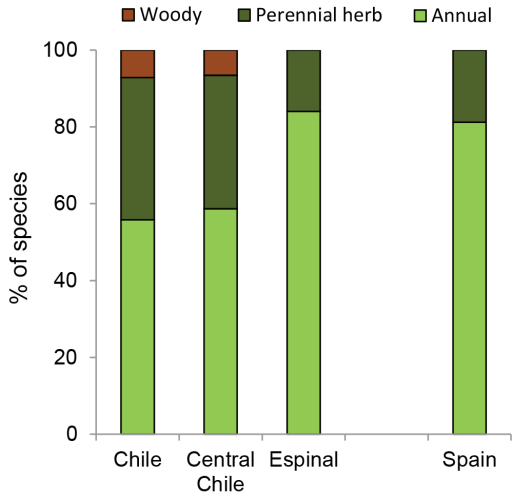

Fig. 10 Frequency histograms of the distribution of non-native species according to their life cycle: annual (ligt green bars), perennial herbaceous (dark green bars) and woody (brown bars) plant. For Chile, the central zone and the *espinal* we only considered non-native species. For Spanish grasslands, we calculated frequency with the total number of species found in the field samplings

In the field samplings we recorded a total of 229 species in the Spanish grasslands and 152 in the Chilean *espinales*, 49% of which were non-native. Of the 10 most common species in Spain, all but one (*Agrostis pourreti* Willd) can be found in the catalogue of non-native species of Chile; moreover, they were found in the sampling in the *espinales* (Table 1). Likewise, of the 10 most common species in the espinales, all but one (*Soliva sessilis* Ruiz and Pav.) are non-native and have been found in sampling conducted in Spain.

Table 1. List of the 10 most frequent species in Spain (a) and in Chile (b). For each species taxonomic family, distribution in Spain and Chile and frequency of appearance in each country are shown.

Species	Family	Distribution	Frequency in Spain (%)	Frequency in Chile (%)
a) Spain				
Plantago lanceolata	Plantaginaceae	Both	42.2	11.4
Bromus hordeaceus	Gramineae	Both	42.8	63.6
Trifolium campestre	Leguminosae	Both	49.7	1.9
Vulpia muralis	Gramineae	Both	50.3	22.2
Hypochoeris glabra	Compositae	Both	50. 6	61. 7
Plantago coronopus	Plantaginaceae	Both	56.9	0.1
Agrostis pourretii	Gramineae	Spain	58. 9	0.0
Trifolium glomeratum	Leguminosae	Both	58. 9	23.1
Tolpis barbata	Compositae	Both	63.1	5.3
Leontodon taraxacoides subsp. longirostris	Compositae	Both	69.4	83.3
b) Chile				
Petrorhagia prolifera	Caryophyllaceae	Both	6.4	33.6
Soliva sessilis	Compositae	Chile	0.0	33. 9
Erodium cicutarium	Geraniaceae	Both	15.8	34.7
Trifolium dubium	Leguminosae	Both	8.3	35.0
Briza minor	Gramineae	Both	4.2	46. 7
Erodium botrys	Geraniaceae	Both	3.3	49.7
Hypochoeris glabra	Compositae	Both	50. 6	61. 7
Bromus hordeaceus	Gramineae	Both	42.8	63.6
Aira caryophyllea	Gramineae	Both	8.8	64.4
Leontodon taraxacoides subsp. longirostris	Compositae	Both	69.4	83.3

DISCUSSION

Arroyo et al. (2000) and Figueroa et al. (2004) consider that in continental Chile there is a total of 707 naturalized non-native species and subspecies. This value is somewhat higher than the 698 taxa considered in this paper, approximately 12% of the total flora. Despite the fact that some recent introductions have been done, a greater amount of species have been excluded from the list due to being spurious citations. The amount of exotic species in Chile, however, is likely higher, considering the little botanical prospection conducted in certain parts of the country. Thus, during the sampling and in view of the lack of confirmation, at least 5 species had not been previously cited: *Aphanes microcarpa* (Boiss. and Reut.) Rothm., *Logfia minima* (Sm.) Dumort., *Moenchia erecta* (L.) G. Gaertn., B. Mey. and Scherb., *Trifolium cernuum* Brot. and *Vulpia ciliata* Dumort. Considering only the central Mediterranean zone, Figueroa et al. (2011) recognized 2395 native species and 507 non-native ones, which account for 18% of the flora in this region (Arroyo and Cavieres 1997; Arroyo et al. 2000). In this case, our data contain 548 non-native species in the central zone, a difference possibly associated with the geographic definition of this zone. This non-native flora contains a large number of families, none of which show any clear dominance, although the most common ones are Poaceae, Asteraceae and Fabaceae, in accordance with the three most invasive families worldwide (Pyšek 1998).

Most of Chile's non-native species are annual plants (56%) of Eurasian-Mediterranean origin (68%). The dominance of exotic annual species coincides with the findings of other authors for other Mediterranean-climate regions (Le Floc'h 1991; D'Antonio and Vitousek 1992; Cowling et al. 1996; Figueroa et al. 2004; Norton et al. 2007). Their rapid growth and high reproduction rates, and capacity to resist unfavorable periods in the form of seeds make them more competitive in repeatedly disturbed open spaces, such as those created by fire, plowing or grazing (Le Floc'h 1991; Gómez-González et al. 2010). As for biogeographical origin, our results show that they are preferentially from the Mediterranean Basin or, in a broader sense, Eurasia, which would coincide with the findings of several authors for Chile and other Mediterranean-climate areas (Montenegro et al. 1991; Arroyo et al. 2000; Holmgrem et al. 2000; Figueroa et al. 2004; Castro et al. 2005).

The annual character and Mediterranean origin predominating in non-native Chilean plants could be related to the different use history from that of the Mediterranean Basin. The pastures of the Mediterranean basin have been subjected to an intense grazing regime involving bovines and other domestic herbivores for over 6,000 years of its evolutionary history (Perevolotsky and Seligman 1998). This long history of coexistence with natural and anthropic disturbances has determined processes of co-evolution between plants and agriculture (Di Castri 1981; Cowling et al. 1996; Perevolotsky and Seligman 1998; Holmgren 2002; Hayes and Holl 2003, Kimball and Schiffman 2003; Ricotta et al. 2009; HilleRisLambers et al. 2010), which have selected the plants presenting more competitive traits in a context of continuous grazing such as, for example, forms of growth, concentration of nutrients in tissues or position of growth meristems, among others (Adler et al. 2004; Díaz et al. 2007). On the contrary, Chile's Mediterranean region underwent a drastic transformation since the colonization only 500 years ago and its native flora might not have co-evolved with large herbivores in the last 10,000 years. This lack of adaptation to continuous grazing means that, with the introduction of livestock, native species are negatively affected, which favors the establishment of alien species (Milchunas and Lauenroth 1993; Holmgren et al. 2000; Adler et al. 2004; Díaz et al. 2007).

The flora of Central Chile is a good expression of the country's as a whole with regard to percentages of the most represented families, life cycle and origin of non-native species. This central zone, representing only 20% of Chile's territory, contains 80% of all the country's exotic plants. This high concentration of naturalized

plants (Matthei 1995) can be accounted for by a conjunction of factors relating to history, environment and land uses. Chile was conquered by land from the north through the Atacama Desert into the central zone. To the south of the Bío-Bío river, the territory was not colonized until just over a century ago (Aronson et al. 1998). Given the arid and semiarid conditions of the North, only the central zone, with its Mediterranean climate, was suitable for agriculture and for 350 years, the species introduced were therefore relegated to this region (Fuentes et al. 2008). It was only as from the XX century that non-native species were introduced into the whole country, with mass and intense deforestation of the austral temperate forest (Donoso and Lara 1996). In short, it is the central zone that has undergone the biggest change as a result of intensive agriculture for over five centuries (Montenegro et al. 1991, Matthei 1995). Moreover, it is the most densely populated region (78% of the country's population, with an average of 75 inhabitants/km^2; Pauchard et al. 2006; INE 2007) and with the densest roads network (Arroyo et al. 2000).

The representation of the non-native flora tends to be greater at more detailed spatial scales (Gaertner et al. 2009), a fact that can be seen in the *espinales* studied. On one hand, the percentage of non-native species therein is much higher than the 13% for the whole country or the 18% for the central zone, reaching 49%. This value is higher than the 36.8% reported by Figueroa et al. (2011) for *espinales* and very similar to that reported by Montenegro et al. (1991). At family level, the percentages of Caryophyllaceae, Rosaceae, Geraniaceae and Rubiaceae double and even quadruple the values characteristic of the country or of the central zone. On the other hand, among non-native species, annual plants show an increase from 56% for the whole country to 84%; exotic woody species were absents from our study. Finally, compared with the 68% of species of Eurasian or Mediterranean origin in Chile, the *espinales* account for 97%. In this context it is interesting to highlight the relationship between regions of origin and species' biological cycle, with a positive association among annual plants for species from the Mediterranean Basin and among woody plants for those of Australian, African or American origin. This relationship is possibly associated with the way in which the species were introduced into the country and with the climatic characteristics of the recipient habitat: unintentionally in the case of most of the plants associated with agriculture and livestock farming (Mediterranean annual plants adapted to grazing; Holmgren 2002) or for ornamental or forestry purposes (woody plants generally of extra-European origin; Pyšek et al. 2011). The extreme values found in the *espinales* (compared with the rest of Chile) referring to distribution of families, biogeographic origin and life cycle are, however, of the same order of magnitude as those found in Spanish grasslands (although proportionally Rubiaceae, Rosaceae and Geraniaceae present higher percentages in Chilean *espinales* and Brassicaceae in Spanish grasslands). Given that Europe, and specifically the Mediterranean Basin, have constituted the main source of immigration since America was discovered (Di Castri 1991; Figueroa et al. 2004; Jiménez et al. 2008) the floristic similarity between both countries appears to indicate that the *espinales* represent a copy of Europe's agricultural model, in which not only animal and plant species (livestock, cereals and associated weeds) were introduced from Europe, but also technology (plowing, harrowing, animal traction) and the culture associated with management of the system (fallow, rotation). The final result is an agroecosystem, the Chilean *espinal*, which not only presents great physiognomic and functional similarity with the Spanish *dehesa* (Ovalle and Avendaño 1987; Ovalle et al. 1990), but is also similar with regard to the floristic characteristics evaluated in this research. There are, however, differences between these two agroecosystems, particularly with regard to species richness (much higher in Spain). It is known that the number of alien species becoming established in a given country is lower than the amount that might potentially arrive (Malo and Suárez 1997) and the number of exotic species capable of reaching Chile is estimated at between 7,070 and 35,400 (Castro et al. 2005). An example is the Santiago Botanic Garden which, in the middle of the XIX century, cultivated over 2000 exotic species, 43 of which became naturalized (Matthei

1995; Castro et al. 2005). These data place in doubt whether the flora of the *espinales* constitutes an impoverished version of Spanish grasslands because specific filters existed that limited the number of species arriving or, on the contrary, whether there is a predominance of the biotic and abiotic filters acting in the assemblage of communities in the *espinales*.

The entry of alien species and the extinction of native ones in a region have been considered a process of global biological homogenization (McKinney and Lockwood 2001; Olden 2006; Olden and Rooney 2006; Winter et al. 2009). Castro and Jaksic (2008) conclude that this homogenization process is not yet significant in Chile, given that from colonization times up to the present, only two species have become extinct (*Plazia cheiranthifolia* (Remy) Wedd. and *Menodora linoides* Phil.) and that the floristic similarity among regions has not significantly changed. Our data, however, and those provided by Jiménez et al. (2008) and Figueroa et al. (2011), would seem to suggest that at least the *espinales* are being subjected to an intense homogenization process, as can be seen in the dominance of certain species (and families) common to Spanish grasslands on the list of most frequent species in the *espinales*. The most frequent species is *Leontodon taraxacoides* (Vill.) Mérat, first recorded in Chile in 1963 (Castro et al. 2005), which contradicts the hypothesis that the exotic species appearing subsequent to 1950 present a narrower range within the country (Arroyo et al. 2000; Pauchard et al. 2004; Castro et al. 2005). This would appear to indicate that this homogenization process has become accentuated in the last few decades.

At present the speed of change of many ecological, economic and social parameters is reaching heretofore unknown rates, and the predictions are even more drastic in reference to changes in land uses at global scale (Lugo and González 2010; USDA 2006). In this context of global change, there is a pressing need to understand these processes of species colonization and naturalization. The exchange of species, successful establishment of some of them or extinction of others undoubtedly contributes to the appearance of new environmental scenarios, with socioeconomic repercussions that are difficult to evaluate in the short term (Rockstrom et al. 2009). Identifying changes in ecosystem structure and functioning in the short, medium and long term constitutes a fundamental objective with regard to evaluating the "health" of ecosystems, as is stated in the objectives of the Millennium Ecosystem Assessment Programme (MA 2003; Carpenter et al. 2009).

Naturalización transcontinental de especies herbáceas en pastizales mediterráneos españoles y chilenos

Transcontinental naturalization of herbaceous species in Spanish and Chilean Mediterranean grasslands

Chapter 2 Where do we come from and where are we going: source and recipient areas

"A people without the knowledge of their past history, origin and culture is like a tree without roots"

Edward Morgan Forster

"All things must come to the soul from its roots, from where it is planted"

Santa Teresa de Avila

Adapted from: Casado MA, Acosta-Gallo B, Sánchez-Jardón L, Martín-Forés I, Castro I, Ovalle C, del Pozo A, de Miguel JM. 2015. Interactive effects of source and recipient habitats on plant invasions: distribution of exotic species in Chile. Diversity and Distributions 21:609-619

INTRODUCTION

The introduction of exotic species is considered one of the biggest threats to biodiversity at global scale (Vitousek et al. 1996). In the last twenty years, great efforts have been made to understand the main drivers of invasion success in a wide range of ecosystems (*e.g.* Richardson and Pyšek 2012). Different authors have highlighted the preponderant effects of environmental control (*e.g.* the climate filtering hypothesis; Weiher and Keddy 1999), habitat characteristics (*e.g.* the fluctuating resource availability theory; Davis et al. 2000) or anthropogenic disturbances (*e.g.* the propagule pressure hypothesis; Lockwood et al. 2005) upon the invasibility of a community or an ecosystem. The lack of agreement regarding what factor is most relevant appears to indicate that invasibility results from the joint action of multiple biotic and abiotic factors, along with human activity (Chytrý et al. 2009) and their importance is site- and/or scale-dependent (Lloret et al. 2005; Funk and Vitousek 2007; González-Moreno et al. 2014).

Analyses of the success of exotic species usually take into account the characteristics of the recipient areas, but less attention has been paid to their performance in their regions of origin (Hierro et al. 2005). Nonetheless, the success of European plants in colonizing non-European regions has been related to their original environment (Prinzing et al. 2002), the cultural and climatic proximity of the source and recipient areas (Lambdon et al. 2008) and pre-adaptations of the introduced species (Pyšek and Richardson 2007; Dostál et al. 2013). Despite this, little is known about the habitat characteristics of the donor communities that act as a source of exotic species in the newly invaded region (Hejda et al. 2009). Kalusová et al. (2013) recently pointed out that European species introduced to North America tend to invade habitats similar to the ones they occupy in their places of origin. This study, however, does not include semi-natural or man-made habitats, which, as the authors recognize, usually contain higher numbers of invasive species than natural habitats.

The level of invasion of species in the ecosystems of the Mediterranean Basin is lower than those recorded in other Mediterranean regions worldwide (Greuter 1994). This difference has been associated with the long history of human presence and of prehistoric invasions in the Mediterranean Basin, which have undoubtedly contributed to the relevant role its ecosystems play as species donors during the transport of organisms from Europe to America, during the colonialism (di Castri 1989). Chile's flora currently comprises a mixture of native and exotic species; 743 non-native plants (14% of its flora), predominantly herbs (Fuentes et al. 2013) of European origin and fundamentally from the Iberian Peninsula (Groves 1986), have been quantified. The process of plant naturalization of European species in Chile started in the colonialism period (XVI century), when the Spanish introduced many exotic species associated with cereal crops and activities related to livestock farming (Martín-Forés et al. 2012). This process was especially noteworthy in the Mediterranean climate region of central Chile, which, despite occupying only 20% of the territory, contains 80% of all the country's exotic plants (Martín-Forés et al. 2012).

In the present study we analyzed the association of Chile's non-native herbaceous flora with the habitat characteristics of these species on the Iberian Peninsula (Spain and Portugal). As a consequence of the environmental and historical-cultural similarities, both regions share different biomes and habitats, as well as numerous species. Moreover, the broad latitudinal range occupied by Chile enables analysis of the relative success of exotic species in relation to their distribution throughout different climatic environments. All this provides an excellent scenario for comparing and analyzing the process of colonization from the source area to the recipient area at different scales and in different climatic environments.In this chapter we attemptedto determine i) whether the distribution of exotic species is conditioned by the climatic characteristics of the

recipient area (Chile); and ii) whether their success can be predicted by means of the habitat characteristics of the donor communities in the source area (Iberian Peninsula). For this purpose we analyzed a wide range of relevés from the Iberian Peninsula, classifying them according to their habitat characteristics (bioclimate, soil nutrient status and type of community associated with human activities).

MATERIAL AND METHODS

Study area

Continental Chile presents an area of 748,012 km^2, with a length of 4,270 km from parallel 17°30' S to parallel 56°32' S. Chile's latitudinal range, its relief and oceanic influence are the main factors explaining its climatic variability. The north presents a desert climate, with little precipitation and an average temperature of around 20 °C. From the Aconcagua valley (Valparaíso region, ~33° S), to Concepción (Bío-Bío region, ~36° S), the climate is Mediterranean, varying from semiarid to subhumid (ranging from 150 to 1200 mm of annual precipitation). Rainfall increases in the southern zone, which exhibits a rainy maritime climate from Temuco (Araucanía region, ~38° S), to the coast of Aysén (Aysén region, ~45° S). In the Austral zone, there is a cold, typical steppe climate, characterized by a broad thermal range, low winter temperatures, and a decrease in precipitation. Besides this latitudinal variation, the existence of the Andes gives rise to an altitudinal temperature gradient that decreases from west to east.

The Iberian Peninsula comprises three countries: Portugal, Spain and Andorra. It has an area of 583,254 km^2, from parallel 43°48'N, at Estaca de Bares point, to 36°0'N in Tarifa. The climate also varies greatly across the whole territory as a response to latitudinal changes, the mountainous relief and the distance to the ocean. The Mediterranean climate predominates throughout the peninsula, with oceanic or continental variants. Arid or semiarid climates, with less than 300 mm of annual precipitation, exist in some enclaves of the peninsular southeast. The Cantabrian range acts as a transition to the temperate climates in the peninsular north, characterized by cool temperatures and abundant precipitation (above 2000 mm yearly) throughout the year.

Data from Chile

A database was created which included all exotic plant species present in continental Chile. We used the Catalogue of Chilean flora by Marticorena and Quezada (1985) and information available from the Laboratory of Biological Invasions of the University of Concepción (Fuentes et al. 2013; http://www.lib.udec.cl/database.html) as basic data. Only herbaceous species (including climbing plants) were considered in the study, because the success of the naturalization process can be influenced by life form (Tecco et al., 2010), and most (around 90%) exotic species have this life form (Fuentes et al. 2013). Moreover, unlike woody species, their introduction is not usually intentional (Pyšek et al. 2011). We assigned a region of origin and current distribution within Chile to each exotic species. Different regional floras were employed to assign region of origin: Flora Iberica (Castroviejo et al. 1986-2013), Flora Europaea (Tutin et al. 1964-80) and Flora del Cono Sur (Zuloaga et al. 2008). As regions of origin, the three large continents were considered: Eurasia, Africa and America (Australasia was not considered because it only included 4 species: *Atriplex semibaccata, Atriplex suberecta, Cotula australis* and *Tetragonia tetragonoides*). Apart from these large geographical regions, the Mediterranean Basin (SE, S and SW Europe, N Africa and SW Asia) was considered independently, given its importance as a source of exotic species to Chile (Castro et al. 2005). A fifth category grouping species of broad distribution (Holarctic, cosmopolitan or sub-cosmopolitan species)

was also included. As for distribution in Chile, each exotic species was assigned to the Chilean administrative regions in which it is currently found. We used the thirteen administrative regions valid until 2007, because the available data are associated with this prior administrative division. These data, together with the minimum time of residence in Chile of the exotic species, were obtained mainly from Castro et al. (2005), Zuloaga et al. (2008) y Fuentes et al. (2013).

Data from the Iberian Peninsula

Data from 12,573 relevés were obtained by means of extensive bibliographic revision and from the SIVIM (Iberian and Macaronesian Vegetation Information System; http://www.sivim.info/sivi/). Although the phytosociological relevés present sampling bias related to their distribution and area covered (Chiarucci 2007), they constitute a useful source of data for exhaustive characterization of vast territories (Janzen et al. 2011). Only relevés performed in communities dominated by herbaceous plants were considered (Fig. 11). We excluded relevés from high mountain areas or the ones associated with unusual substrates (dunes, halophiles). The area of the relevés was variable (mode 10 m^2, range 0.1 - 600 m^2), which is frequent in European phytosociological studies (Chytrý and Otypková 2003). We only considered herbaceous species (including climbing plants). Species synonymies were standardized and the database was simplified to species taxonomic level; subspecies, groups of species and hybrids were excluded. Species origin (native or introduced to the Iberian Peninsula) was assigned to each species according to Castroviejo et al. (1986-2013) and Tutin et al. (1964-80).

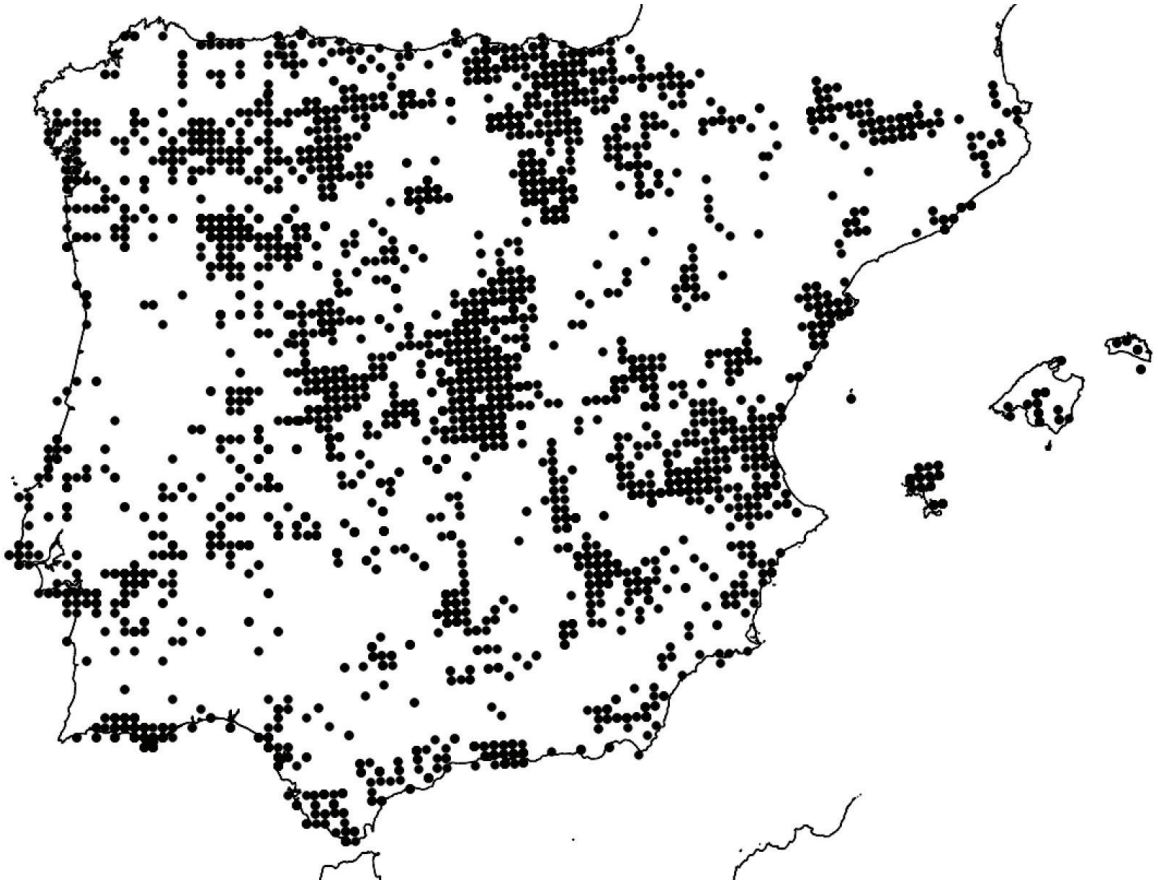

 Fig. 11 Map of the Iberian Peninsula showing the distribution of the 11,702 relevés used in this study

Relevés as phytosociological units consider combinations of plant species (communities) coexisting in similar habitats and under similar biogeographical and successional conditions. We characterized each relevé considering three habitat characteristics: bioclimate, soil nutrient status, and type of community. The bioclimate categories were Mediterranean, temperate or both, depending on whether the community was associated with one of each bioclimate or it was present in both types. Soil nutrient status (with two categories: high and low, corresponding to nitrophilous or non-nitrophilous communities, respectively, *sensu* Rivas Martínez et al. 2002) represents the community's capacity to grow in soils with high or low nutrient availability, respectively. Finally, as type of community we differentiated four categories based on their association with human activities: ruderal (communities usually associated with disturbed sites, such as roadside verges or urban areas, and usually comprising nutrient-demanding species), weed (wild plant communities associated with arable lands), grassland (communities associated with livestock activities) and woodland fringe (shade-loving herbaceous communities associated with forest and shrub edges). We assigned the categories to each relevé taking into account the characterizations of the phytosociological class or its lower-level orders, alliances or associations (Rivas-Martínez et al. 2002).

Data analyses

In a first step we used the Chilean database with all herbaceous exotic species, regardless of their region of origin. In order to classify Chile into internally homogeneous regions with regard to the distribution of its exotic species, we performed a cluster analysis of the matrix of administrative regions x exotic species presence. In the analysis we used Yule's coefficient as a similarity index and the centroid as classification algorithm. We subsequently assigned a geographic sector (the set of administrative regions in Chile included in a given group in the cluster analysis) to each species when its current distribution was restricted to this sector; the species present in more than one geographic sector were grouped as species with a broad distribution in Chile. We analyzed the association between geographic sectors detected by cluster analysis and the region of origin of species (Chi-square test on contingency tables and post-hoc z-test) and the minimum time of residence (Kruskal-Wallis test).

In the second step, we selected the subset of exotic species native to the Iberian Peninsula from the Chilean database - species naturalized both to Chile and to the Iberian Peninsula were omitted. For each relevé we calculated the number of species in common with Chile considering each geographic sector separately. Species richness in the relevés was highly variable (average = 15.5, range from 1 to 69), partly because of the different areas considered in the relevés (the log-log area-species richness relationship was highly significant but with little explanatory power: $r = 0.230$, $p < 0.0001$, $R^2 = 5.3\%$). To minimize the influence of the species richness of the relevé, we transformed the number of common species into a percentage over the total of the relevé's species richness (Chytrý et al. 2008; Kalusová et al. 2013). A total of 871 (7%) relevés with less than 6 species (10th percentile) was excluded from the analysis to avoid discretization of the percentage value obtained, and therefore, 11,702 relevés were finally used.

We used the percentage of species in common with Chile as the response variable in all subsequent models. This variable did not exhibit normal nor homoscedastic distribution in Chile's geographic sectors, even after transformation, and we therefore employed non-parametric analyses . We performed analyses for each geographic sector separately. We applied the Kruskal-Wallis test to analyze the relationship between the percentage of common species and the three habitat characteristics of the relevés (predictors: bioclimate, soil

nutrient status and type of community). We employed regression trees to analyze the existence of interactions among these predictors in order to explain the percentage of species in common (response variable). Regression trees involve a non-parametric technique that is well suited for analyzing complex ecological data and non-additive effects and which enables the importance of the variables considered to be hierarchized. Data is split into increasingly homogenous groups based on the predictor variable at each split that explains the greatest deviance of the dataset. There are no assumptions regarding data distribution, and the trees are not influenced by missing data, outliers, or monotonic transformations of the predictor variables. This analysis can detect non-linear relationships, explain complex interactions, and is robust in relation to outliers and missing data (De'ath and Fabricius 2000). We performed regression trees with SPSS 19 and used CRT as the growing method, cross validation, a minimum number of cases in each subsidiary node of 150, as well as a minimum improvement value of 0.01.

RESULTS

We considered 645 herbaceous exotic species in Chile. Of these, 478 (74%) were also found in the relevés of the Iberian Peninsula, 73 of which were exotic to both regions. Classification of Chile's administrative regions according to the presence of exotic species provided four large groups or geographic sectors (Fig. 12). The distribution of these sectors fitted well to the latitudinal climatic variation: sector S1 (from the Arica to the Coquimbo regions, presenting an arid tropical or semiarid Mediterranean climate), S2 (from the Valparaíso to the Maule regions, displaying a humid or subhumid Mediterranean climate), S3 (from the Bío-Bío to the Lagos regions, which presents a temperate climate) and S4 (Aysén and Magallanes regions, with a cold temperate or anti-boreal climate). Given the altitudinal climatic influence of the Andes, we assigned climate to each sector taking into account only areas at low and medium altitude, which are the ones with the highest number of exotic species (Alexander et al. 2011). We considered a fifth group, S5, for species present in at least two of the groups in the cluster. This group of broadly distributed species was the one presenting the highest number of exotic species (47%), followed by groups S2 and S3 (Table 2). Most species in group S5 were present in four (31% of species) or three (55%) geographic sectors. Considering all exotic species (those exclusive to each sector plus the widely distributed ones) the highest concentration occurred in groups S2 (419 species) and S3 (401 species). The species included in each of the five geographic sectors differed in the time since they were first recorded in Chile (Kruskal-Wallis 87.463, $p<0.0001$), although the post-hoc comparisons only differentiated the broadly distributed group (S5, mean residence time of 129 ± 2.8 years) from the other four (mean residence time from 71 to 84 years). Likewise, we detected a significant association (Table 2) between the geographic sectors and the regions of origin of the exotic species in the sector, except for the one corresponding to the temperate climate (S3) in which the exotic species are from different regions of origin. The species from America and Africa were positively and significantly associated with the sector presenting an arid tropical or semiarid Mediterranean climate (S1). The sector displaying a Mediterranean climate (S2) was characterized by a predominance of species from the Mediterranean Basin and, to a lesser degree, from Africa. The sector exhibiting a cold temperate climate (S4) basically presented species with a broad distribution and Eurasian ones, the latter being dominant also in the sector including the species with a broad distribution throughout Chile (S5).

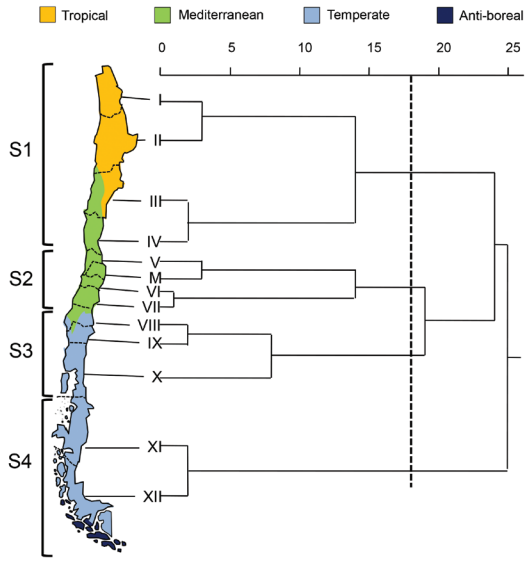

Fig. 12 Cluster analysis of Chile's administrative regions (Roman numerals) based on the presence of exotic species. The colors on the map represent the macro-bioclimates (according to Luebert & Pliscoff 2006, modified). S1 to S4 represent the geographic sectors (groups of the cluster analysis) identified in this study. The sector including the broadly distributed species (S5, species present in at least two of the groups of the cluster) is not represented. The regions correspond to I: Arica and Parinacota/Tarapacá; II: Antofagasta; III: Atacama; IV: Coquimbo; V: Valparaíso; M: Metropolitana; VI: O'Higgins; VII: Maule; VIII: Bío-Bío; IX: Araucanía; X: Los Lagos/Los Ríos; XI: Aysén; and XII: Magallanes

Table 2. Number of exotic herbaceous species (percentage in brackets) in Chile according to the geographic sector (S1 to S5, see Fig. 12) in which they are found. For each geographic sector, the area and the percentage of species according to region of origin is indicated. Different letters between the regions of origin indicate significantly different values (z-test, $p>0.05$), whereas the positive associations (corrected residual >1) between region of origin and geographic sector are highlighted in bold. NA: not applicable.

Sector	Area (km2)	Species	Region of origin				
			America	Africa	Mediterranean	Eurasia	Wide
S1	300,904	60 (9.3)	**46.9**^{b}	**6.9**^{ab}	20.7^{cd}	10.3^{d}	15.5^{ac}
S2	78,482	125 (19.4)	18.5^{abc}	**4.8**^{ab}	**40.3**^{a}	27.4^{bc}	8.9^{c}
S3	135,924	109 (16.9)	18.2^{a}	3.7^{a}	34.9^{a}	35.8^{a}	12.8^{a}
S4	240,792	47 (7.3)	2.1^{b}	0.0^{b}	31.9^{a}	**42.6**^{a}	23.4^{a}
S5	NA	304 (47.1)	13.9^{b}	1.7^{b}	31.7^{ab}	**38.3**^{a}	**14.5**^{ab}
Total	756,102	645 (100)					

When the relevés were classified according to their habitat characteristics, the percentage of species in common with Chile varied with the geographic sector (Fig. 13). Considering soil nutrient status, in S1, S2 and S3 a higher percentage of the species comes from communities associated with high soil nutrient status habitats, whereas in S4 the species were predominantly from soils of low nutrient availability (Fig. 13a). These changes were also observed in the percentage of species associated with communities from Mediterranean bioclimate (higher in S1 and S2) to those from both climates (S3) or with species from a temperate one (S4; Fig. 13b), as well as in the percentage of species from ruderal and weed communities (higher in S1 and S2) to those from woodland fringe (higher in S3 and S4; Fig. 13c). In sector S5 the highest number of species in common comes from ruderal communities characterized by high soil nutrient status in temperate climates or indifferent to climate conditions.

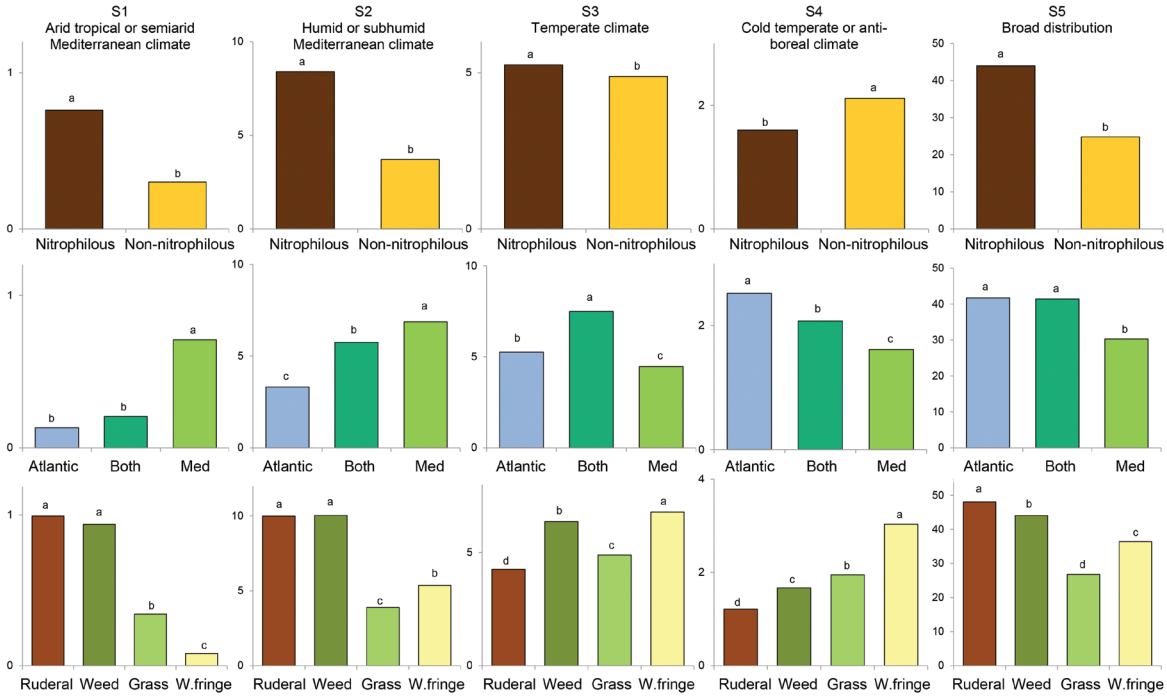

Fig. 13 Average percentage values for species in common with Chile for the relevés from the Iberian Peninsula classified according to their a) soil nutrient status (high/low), b) bioclimate (Mediterranean/temperate/present in both climates) and c) type of community (ruderal/weed/grassland/woodland fringe). Med. indicates Mediterranean climate, and Grass. indicates grasslands communities. The letters mean significant differences (Kruskal-Wallis, $p<0.05$) among the categories of each variable. The analyses were performed for each geographic sector (from S1 to S4, see Fig. 12), and for the broadly distributed species (S5)

The regression trees enabled us to hierarchize the relevance of each variable of the donor habitat in each of the five geographic sectors identified and to detect the combination of variables that determined the highest percentage of species in common (Fig. 14). In all the sectors, type of community constituted an important variable, determining the first split in three of the geographic sectors and the second split in one sector. Bioclimate determined the first split in S3 and the second split in the four remaining sectors. Finally, nutrient status was the least important variable but established the first split in S5. The combination of variables determining the highest percentage of species in common with Chile always included the type of community, but with different climate conditions for each geographic sector. Thus, in the more arid sector and the one presenting a Mediterranean climate (S1 and S2), the communities that acted as the main donors were ruderal or weed ones from Mediterranean climates in their regions of origin. On the contrary, in the sectors with temperate (S3) or especially anti-boreal climates (S4), woodland fringe communities from temperate climates played a more significant role. As regards the group comprising the broadly distributed species (S5), the relevés presenting the highest percentage of species in common came from ruderal, weed and grassland communities with a high soil nutrient status from temperate climates.

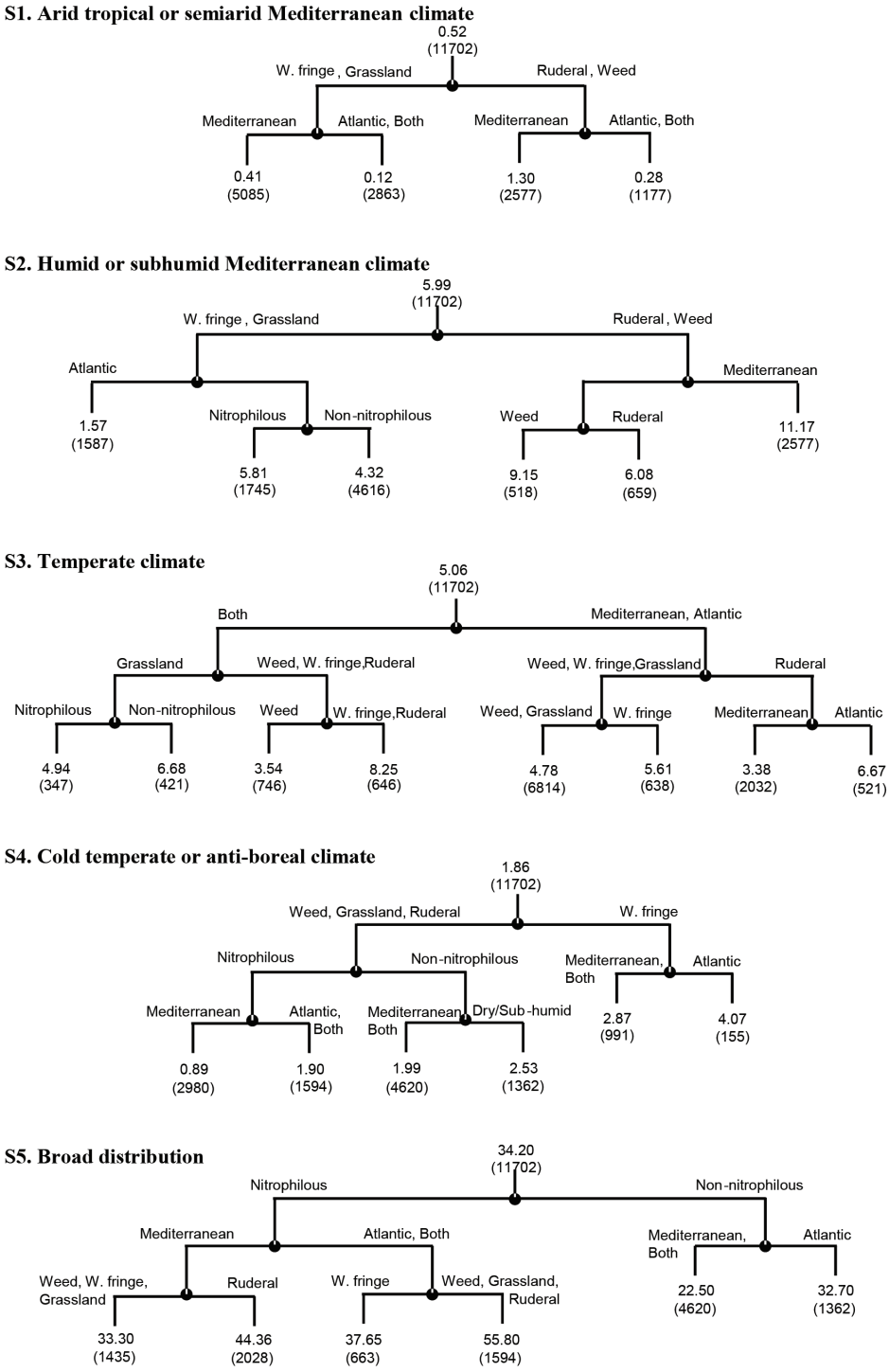

Fig. 14 Regression trees for percentage of exotic species in Chile in the relevés classified according to, bioclimate (Mediterranean/temperate/present in both climates), nutrient status (high/low) and type of community (ruderal/ weed/grassland/ woodland fringe) on the Iberian Peninsula. Each geographic sector of Chile (S1 to S5, see Fig. 12) was considered separately. Values above the upper node and under each final node are average percentage values of common species in Chile for cases within that group, while values in brackets represent the number of cases for that group

DISCUSSION

Chile shares almost three quarters of its herbaceous exotic flora with the species recorded in the set of selected relevés from the Iberian Peninsula. Even at community level, 18% of the relevés present over 75% of species in common with the Chilean non-native flora. This floristic similarity highlights the role the Iberian communities play as donors, and represents an ideal scenario for analyzing the interactive effects of both source and recipient areas in the naturalization process. The spatial scale used in each country differed greatly (community scale for Spain and regional scale in Chile) which prevents characterization of both datasets with the same accuracy. However, combined study of the distribution of exotic species in Chile and of the characteristics of the Iberian communities acting as donors provides an understanding of some of the drivers that have determined the successful establishment of some of these species in Chile.

Importance of climate in the recipient area

Our results indicate that the climate of the recipient area plays a crucial role in the current distribution of Chile's exotic species. It should be pointed out that half of these species are restricted to only one climatic region in Chile. The distribution of these species among the different regions is not homogeneous; they are less abundant at both ends of the climatic gradient: the arid tropical climate in the north and the cold temperate climate in the south. This "resistance" to naturalization in extreme climatic conditions is widely recognized (Alpert et al. 2000; Davis et al. 2000; Chytry et al. 2008b, 2009) and is responsible for the latitudinal (Sax 2001; Bannister et al. 2012) and altitudinal (Pauchard et al. 2009; Haider et al. 2010; Alexander et al. 2011) gradients of decrease of exotic species.

Central Chile, despite its small area, concentrates most of the country's exotic species (Arroyo et al. 2000; Castro et al. 2005; Fuentes et al. 2013). In our study this area (corresponding mainly to geographic sector S2) not only includes 65% of Chile's exotic herbaceous species but also exclusively contains almost one third of them. It exhibits a Mediterranean or temperate climate, and it is also the region in which the Spanish historically settled and developed European agriculture (Martín-Forés et al. 2012), and has become the most highly populated region with the largest area of grasslands and arable land (Arroyo et al. 2005). The co-variation between climatic factors and anthropic pressure makes it difficult to establish whether this high richness of exotic species is a direct consequence of a more benign climate or whether this relationship derives from, or has been potentiated by, the existence of more anthropized habitats (Chytrý et al. 2008; Lambdon et al. 2008; Pyšek et al. 2010).

The other half of the exotic species is included in the widely-distributed group. These are generalist species capable of growing in a broad range of climates and which display greater phenotypic plasticity (Richards et al. 2006; Davidson et al. 2011); they are therefore better endowed to spread and to colonize different types of habitats and even to become invasive (Parker et al. 2003). Interestingly, they correspond to the species presenting a longer time of residence, which have therefore availed of more time to overcome the lag phase (Caley et al. 2008), and to disperse and colonize new territories. Residence time can be considered as a proxy for propagule pressure (Richardson and Pyšek 2012) and it is well documented that species with longer residence times are more widespread (*e.g.* Castro et al. 2005; Wilson et al. 2007).

Influence of the source area on exotic species distribution

Climate in the recipient region constitutes an effective filter for the distribution of exotic species in Chile. There are, however, other factors related to the source areas that equally condition the success of these species in becoming established. Our results enable us to evaluate the influence of these factors at two scales: a broad geographic one, associated with the regions of origin of the exotic species, and a more detailed one, relating to the donor communities of these species on the Iberian Peninsula.

At broad geographic scale there is a significant association between the geographic (*i.e.* climatic) sectors identified in Chile and the regions of origin of the species therein. In Chile's hot and arid north, there is a predominance of species of African or American origin, fundamentally presenting a tropical or subtropical distribution. The central region, with a Mediterranean climate, is mainly occupied by species from the Mediterranean Basin. Southern Chile, with its cold humid climate is especially occupied by Eurasian species from mid- or high latitudes. The climatic similarity between source and recipient areas indicates that species' climatic tolerance is essential with regard to accounting for successful establishment in a new region (Haider et al. 2010). According to our results, climate acts as the principal predictor of potentiality of species invasion (Kolar and Lodge 2001; Dawson et al. 2009; González-Moreno et al. 2014). This pre-adaptation of introduced species to the environmental conditions of a new region has been highlighted by numerous authors (*e.g.* Pyšek and Richardson 2007; Richardson and Pyšek 2012).

At finer scale, our results demonstrate the different degree of importance of communities on the Iberian Peninsula as donors of species to the different geographic regions of Chile. Habitat characteristics, such as those related to climate, soil nutrient status and human activities appear to affect the potentiality of a community to act as a donor of exotic species. The relative importance of these factors, however, ultimately depends upon the climate of the recipient region. At this small scale, one can also observe an unequivocal correspondence between the climatic characteristics of source and recipient areas: Chile's arid regions, or those presenting a Mediterranean climate, have more species in common with Iberian communities associated with a Mediterranean climate, whereas the regions with a temperate or anti-boreal climate have more species in common with communities indifferent to climate or temperate ones. The type of human activities, however, is seen to constitute the main factor responsible for the success of exotic species across different climatic conditions in Chile. Along the Chilean climatic gradient there is a significant change in the main Iberian donor communities, from ruderal or weedy ones to those associated with woodland fringes. This gradient is in correspondence with the distribution of the main land uses throughout the country, from arable land and industrial or urban areas in the north and center of Chile to forestry landscapes in the south. These results highlight the importance of the characteristics of communities in the source areas acting as donors but also the relevance of human pressure as a driver of exotic distribution in the recipient area (Marini et al. 2012). High levels of invasion have been observed in human-made habitats, such as ruderal vegetation and arable land (Lambdon et al. 2008), which are related to the creation of disturbed areas as well as to the increase in propagule pressure (Chytrý et al. 2008).

Only in the group of widely distributed species the type of land use has less importance, assuming soil nutrient status a more prominent role. The more successful (in terms of spatial distributions) exotic species in Chile are the ones adapted to high soil nutrient concentrations, whether by natural or anthropic means. Many authors have highlighted the fact that the more productive or altered habitats are more prone to invasion (Chytrý et al. 2008; Pyšek et al. 2009; Jansen et al. 2011; González-Moreno et al. 2014) and have a greater potential to export

species to other regions (Dostál et al. 2013; Kalusová et al. 2013, 2014). Successful naturalization in highly productive habitats has been associated with the existence of certain functional traits (*e.g.* rapid growth, large specific leaf area, high seed production; Wright et al. 2004) that make species more competitive in rich soils and generally subjected to disturbance (Grime 1979; Dostál et al. 2013). This approach is consistent with the fluctuating resource availability theory (Davis et al. 2000), which suggests that changes in availability of resources constitute a key process when determining the invasibility of a territory (Shea and Chesson 2002; Chytrý et al. 2008).

In summary, the results obtained enable us to interpret the distribution of exotic species in Chile as a process in which the habitat characteristics of the recipient area (climate, human activities, propagule pressure, disturbance) are complemented by the existence of pre-adapted species from the source area. Numerous studies have attempted to determine whether the factors that best determine the level of invasion are climatic ones (Weiher and Keddy 1999; Gaston et al. 2003; Wiens and Graham 2005; Kueffer et al. 2010; Thuiller et al. 2005) or factors related to the characteristics of the habitat (Hejda et al. 2009; Jansen et al. 2011; Marini et al. 2013; Dostál et al. 2013; Kalusová et al. 2013). Our results indicate that both factors come into play, acting jointly and in a hierarchical manner at different scales. Climate determines the possibilities of establishment at broad scale level, and it is time of residence that explains the expansion of exotic species' distribution area. Within each climatic region, the communities acting as the principal donors of species are associated with the habitat characteristics of the source area (particularly human activities). This hierarchy in the effects of environmental factors points to the fact that invasion is context- and scale-dependent (Lloret et al. 2005; Guo et al. 2006; Pyšek and Richardson 2007) and that the differential importance of one factor or another can only be detected if we study territories showing a wide range of environmental heterogeneity (as is the case of Chile) and at different spatial scales (see for example Pyšek et al. 2009).

Naturalización transcontinental de especies herbáceas en pastizales mediterráneos españoles y chilenos

Transcontinental naturalization of herbaceous species in Spanish and Chilean Mediterranean grasslands

Chapter 3 Environmental filtering

"One who gains strength by overcoming obstacles possesses the only strength which can overcome adversity"

Albert Schweitzer

"It's part of life to have obstacles. It's about overcoming obstacles; that's the key to happiness"

Herbie Hancock

Adapted from: Martín-Forés I, Sánchez-Jardón L, Acosta-Gallo B, del Pozo A, Castro I, de Miguel JM, Ovalle C, Casado MA. 2015. From Spain to Chile: environmental filters and success of herbaceous species in Mediterranean-climate regions. Biological invasions 17:142-1438

INTRODUCTION

The coexistence of species with different biogeographic origins has been recognized as one of the most interesting special cases of ecological community assembly processes. Understanding how environmental heterogeneity influences plant diversity is of great importance to basic and applied ecologists (Sutherland et al. 2013) and contributes to improved biological invasion control (Richardson and Pyšek 2006). The number and type of exotic species within a region given introduction history is the result of the combined effects of biotic and abiotic factors (see Seipel et al. 2012 for examples) in both, inside and outside their region of origin, that filter species arrival and dispersal. Plant traits determine the potential for establishment of a species outside its region of origin (Hejda et al. 2009) and the existence of extra-range dispersal mechanisms (transcontinental, transoceanic or long-distance dispersal) that are usually selective (principally favoring species associated with human activities, like ruderal species or those associated with crops) in allowing species to reach new areas (Wilson et al. 2009). Once in the recipient area, other factors act during the phases of dispersal, establishment and persistence of the species (Lilley and Vellend 2009).

A wide range of non-exclusive hypotheses have been proposed to explain the naturalization success of exotic species in a given region (see for example Pyšek and Richardson 2007). Catford et al. (2009) summarize these hypotheses in three big groups: those related to propagule pressure, those associated with physical conditions of recipient community and finally, those which consider biotic relationships. Propagule pressure (Lonsdale, 1999) considers size and frequency of introductions; therefore it heeds multiscale processes that can act from regional to transcontinental scales. Among those considering abiotic filters conditions as key factors in the naturalization process, resource availability is of special importance (*e.g.* Davis et al. 2000; Melbourne et al. 2007). Resource supply reduces competitive pressure, making communities more susceptible to invasion when an increase in unused resources occurs. Alternatively, the naturalization process may be explained by the diversity-resistance hypothesis (Elton 1958; Kennedy et al. 2002), which contends that highly diverse communities are more resistant to invasion, and therefore biotic filters (interaction between native community and exotic species) are determining factors in this process. According to Gilbert and Lechowicz (2005), unsaturated plant communities, or those that have their species richness limited by the regional pool of species available, can be more susceptible to invasion by exotic plant species (Tilman 1997; Moore et al. 2001). However, current knowledge about abiotic and biotic filters in the naturalization process is mainly focused on the recipient area (Guo 2006) which does not allow a precise explanation of different colonization rates by exotic species.

In Mediterranean-climate regions, changes in land use have had a great impact on landscapes and plant diversity (Rundel 1998). In the Mediterranean Basin, anthropogenic modification of the landscape due to grazing, cropping and forest harvesting has been occurring for thousands of years, resulting in plant communities that have co-evolved with human practices (Di Castri 1981; Perevolotsky and Seligman 1998) like, for example, the Spanish agro-sylvopastoral system called *dehesa* (Joffre et al. 1999). Conversely, other Mediterranean areas with much shorter histories of intensive human intervention, like Chilean *espinal* (an anthropogenic savannah mainly formed by *Acacia caven* or *espino*), have undergone a rapid change in land use, threatening their biodiversity (Underwood et al. 2009), and also favoring the invasion by exotic species (Arroyo et al. 2000).

The Chilean *espinal* and Spanish *dehesa* are distributed along a wide range of Mediterranean-type climates. The *espinal* represents a reproduction of the *dehesa* in terms of physiognomy, livestock, management technology and associated culture (Martín-Forés et al. 2012). These ecosystems have great similarities in the structure (a continuous herbaceous layer with scattered trees) although they differ in the species composition,

especially concerning woody vegetation. The *dehesa* represents the source and the *espinal* the recipient area for most of the Chilean exotic species, and therefore constitute an excellent scenario to study the process of colonization and naturalization of exotic species (Pauchard et al. 2004; Jiménez et al. 2008).

The aim of this study is to investigate the role of abiotic and biotic factors on the process of establishment and naturalization of exotic species in Central Chile. Our hypothesis is that abiotic (climate and soil) conditions are key factors acting as filters in both the source (by selecting those species with the highest potential to colonize other areas) and the recipient areas (by determining their success at establishing and spreading). We consider that such abiotic determinants may act differently on species, depending on their region of origin and evolutionary history (natives or exotics), and their capacity of establishment in Chile coming from the Mediterranean Basin. In addition, in the recipient area, success would be conditioned by the interactions with native Chilean species.

MATERIAL AND METHODS

Study area

The study was conducted in the Mediterranean regions of Central Chile and Spain. In Chile, the study was carried out in the *espinal* ecosystem, across an extensive area between 32°31' to 37°00' S and 70°46' to 72°34' W (~600 km long from North to South), with mean annual precipitation ranging between 300-1200 mm. In Spain, the study was conducted in the *dehesa* ecosystem located in the center-west of the Iberian Peninsula (Extremadura, N Andalusia and W Castilla-La Mancha), from 37°51' to 40°14' N and from 4°23' to 7°02' W, and with mean annual precipitation ranging between 400-1100 mm (Fig. 15). Soils in both regions are slightly acidic, derived from igneous or metamorphic rocks and the topography is hilly. In both countries, the land has been used for extensive livestock grazing, especially sheep and cattle.

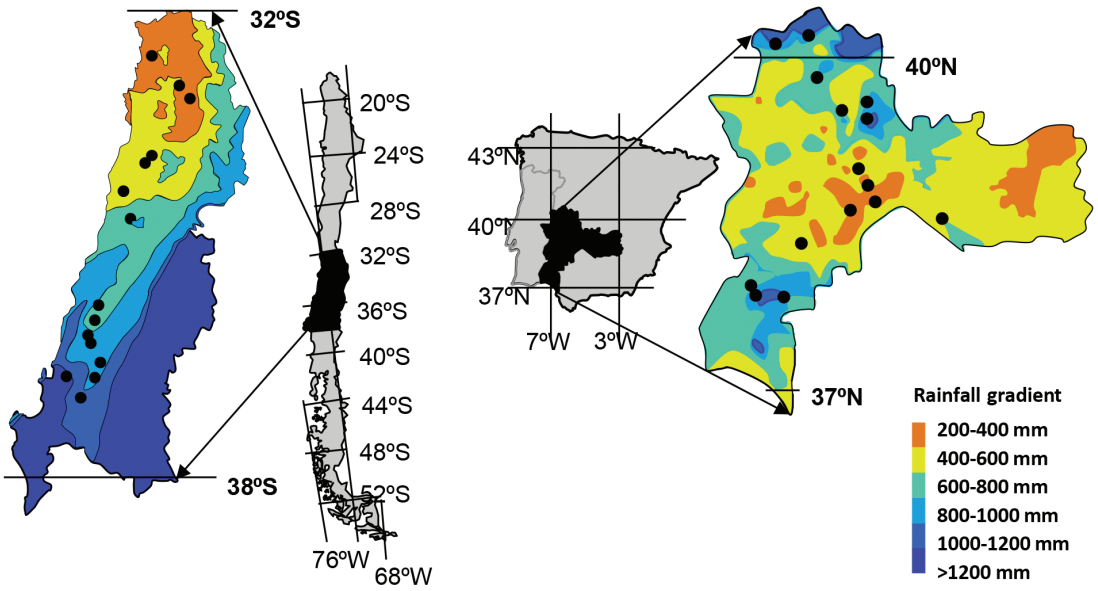

Fig. 15 Map of the studied areas of Mediterranean grasslands in Spain and Chile, including sampling sites. Color tones represent rainfall variability in each country

The *dehesa* contains scattered trees of holm oak (*Quercus ilex subsp. ballota*) or cork oak (*Quercus suber*) within a herbaceous layer comprising mainly winter annuals (Joffre et al. 1999; Gea-Izquierdo et al. 2010). Its origin dates back several centuries, when human intervention in woodlands transformed the landscape into a pseudosavannah (López et al. 2007). *Dehesas* are characterized by a very high plant species richness (Pineda and Montalvo 1995), and cover about 3.5 million ha in South Western Spain (MAPA 2008) and about 0.7 million ha in Portugal (Pereira et al. 2004). The vegetation is adapted to Mediterranean-type climate, characterized by scarce precipitation in summer (drought period from June to September in the Northern hemisphere).

According to Figueroa et al. (2011), the Mediterranean zone of central Chile contains 2,395 native species and 507 exotics that represent 18% of the flora in this region. This proportion increases significantly in the *espinal*, where the percentage of exotic species is much greater (37% and 49% according to Figueroa et al. (2011) and Martín-Forés et al. (2012), respectively). This high proportion of exotic species in Chile can be explained by its history of land use and disturbance. The pre-Conquest vegetation of the actual *espinal* area was a dense mosaic of forests and shrublands, similar to sclerophyll-dominated woodlands in other Mediterranean regions around the world (Di Castri et al. 1981). The arrival of exotic species in the *espinal* has been closely associated with this transformation of the landscape after the European colonization in the 16th century (Aronson et al. 1998; Arroyo et al. 2000; Figueroa et al. 2004). The *espinal* presents various similarities to the Spanish *dehesas*. Its herbaceous layer is composed by annuals, both native and exotic species, mainly originating from the Mediterranean Basin (Ovalle et al. 1990; Ovalle et al. 2006; del Pozo et al. 2006). It comprises an area of about 2 million ha in Central Chile along the eastern slopes of the Coastal mountain range (Ovalle et al. 1999).

Data collection

Vegetation surveys were conducted in the two Mediterranean regions in spring, at the peak flowering periods for most plant species (*i.e.* May and June in Spain, and October and November in Chile). Samplings were carried out during two consecutive growing seasons (2010 and 2011) to detect possible time variation in species abundance from one year to another, which is common in Mediterranean-type ecosystems (Peco et al. 1983; Figueroa and Davy 1991). In each country, 15 sites were selected to cover the whole range of Mediterranean-type climates of each region **(Fig. 15)**. At each site, vegetation was evaluated in two 10 x 10 m plots located on hillside (north-faced and south-faced aspect in Chile and Spain, respectively) and flatland positions, so as to consider possible differences in plant species composition associated with differences in water availability between slope positions (Acosta et al. 2008). In each plot, six 50 x 50 cm quadrats were randomly distributed where the presence of all occurring species was assessed. Quadrats were always situated in open areas to avoid the influence of trees on species composition (Marañón et al. 2009; de Miguel et al. 2013). In the Chilean surveys, only two woody species were recorded: *Baccharis linearis* and samplings of *A. caven*, both natives. In the Spanish surveys, seven woody species were found: *Calluna vulgaris, Cistus crispus, Cistus ladanifer, Halimium umbellatum, Lavandula pedunculata, Quercus ilex* and *Retama sphaerocarpa*, none of them present in Chile. Thus, considering that naturalization success may depend on plant life form (Tecco et al. 2010) and that most of exotic species (around 90%) present herbaceous life form (Fuentes et al. 2013), in the subsequent analyses only herbaceous species were considered.

Chilean species were classified as native or exotic according to Marticorena and Quezada (1985; 1987), and the information provided by the *Laboratorio de Invasiones Biológicas de la Universidad de Concepción* (LIB; http://www.lib.udec.cl/database.html). In the case of Spain, species were classified as 'colonizer in Chile' (hereafter

colonizers); those species that have become naturalized in any Chilean region and therefore are present in the LIB database and 'exclusive of Spain' (hereafter exclusives); those species that might or might not have arrived to Chile, but with certainty they did not establish and become naturalized, thus they are only present in Spain). This definition of exclusiveness refers only to the comparison with Chile. In fact, about 10% of these exclusive species were capable to colonize other Mediterranean areas (*e.g. Aegilops triuncialis, Crassula tillaea* or *Herniaria hirsuta* in California). Three species *Isolepis cernua, Juncus bufonius* and *Montia fontana* are native to both countries, therefore they were considered as natives in Chile and exclusives in Spain. Nomenclature of all species of European origin was standardized according to Castroviejo et al. (1986-2010), and in the case of families as yet unpublished in this source, to Tutin et al. (1964-80). For the Chilean native species, nomenclature was standardized according to Zuloaga et al. (2008).

Climate and soil conditions (hereafter 'abiotic factors') were determined at each site. Climate variables considered were: 1) annual precipitation (PREC, mm), 2) mean annual temperature (TMED, ºC), 3) maximum temperature of the warmest month (TMAX, ºC), 4) minimum temperature of the coldest month (TMIN, ºC), 5) temperature oscillation (TOSC), calculated as the difference between TMAX and TMIN and 6) number of months with drought period or water deficit (MWD), calculated as the number of months in which TMED is at least double than PREC (Baugnols and Gaussen 1953). For Spain, climate variables were obtained from the State Meteorological Agency (AEMET, http://www.aemet.es) and the *Atlas Climático Digital de la Península Ibérica* (Ninyerola et al. 2005). In Chile, climate data were obtained from WorldClim (Hijmans et al. 2005), at a resolution of 30 arc-seconds.

In each of the 60 plots (two countries x 15 sites x two geomorphological positions), five soil cores 5 cm in diameter and 12 cm in depth, excluding the aboveground biomass and litter, were sampled in 2010. The cores were pooled and homogenized, air-dried and sieved through a 2-mm mesh sieve before their analysis. Soil pH, organic matter (SOM, %), N, P, K, S and Al concentrations (ppm), C/N ratio and the percentage of sand, clay and silt were quantified using standard methods (Sadzawka et al. 2006). All soil samples were analyzed employing the same methodology at the Institute of Agricultural Science (Spanish National Research Council of Madrid). Any atypical values in soil variables that exceeded more than three times the interquartile range were replaced by the nearest value observed within the range of data of the same variable. This occurred in 1.5 % of the cases.

Data analyses

In order to obtain a reduced number of factors summarizing climate and soil variability, we conducted a Principal Component Analysis (PCA) for each group of variables. Prior to that, t-tests for mean comparison for each soil and climate variable were conducted in order to assess global differences between countries and to determine whether the PCA should include data from both Chile and Spain, or it should be calculated for each country separately. We preferred to use PCA components instead of the original variables because the components are orthogonal and avoid the high correlation between some variables (*e.g.* temperature and precipitation).

The influence of abiotic factors (climate and soil) on plant species richness was evaluated using generalized linear models with a Poisson error distribution. Models were fitted considering as response variable the richness of each species group in each country: native and exotic species to Chile, colonizer and exclusive species in Spain. We decided to compute data from each country separately in order to provide a comprehensive

model for each species group. Data from the two sampling years were used so as to encompass interannual variation in species occurrence. We computed all the possible models including the slope zone (SLOPE) and the two first axes of the climate and soil PCAs (CLIM1, CLIM2, SOIL1 and SOIL2) as predictors. Taking into account possible non-linear relationships, the respective quadratic terms (CLIM1^2, CLIM2^2, SOIL1^2 and SOIL2^2), were also included. We tested the significance of including site and quadrats nested in sites as random factors in the models by computing the beyond optimal model (including all predictors); because of these mixed-effects models were not significantly different from the fixed-effects model adjusted by REML, only fixed effect models were further calculated for simplicity (Zuur et al. 2009). Analyses were performed in R (R Core Team 2013) using packages lme4 (Bates and Maechler 2010) and glmulti (Calcagno and de Mazancourt 2010).

Models were compared with the Akaike Information Criterion corrected for small sample size (AICc) (Burnham and Anderson 2002). We selected the 100 models with lower AICc values and we calculated the Akaike weight of each of these models, according to Burnham and Anderson (2002). For this subset of models, the relative importance of each predictor (Wi) was calculated as the relativized sum of the Akaike weight of the models in which this predictor appears (Burnham and Anderson 2002). Relevant predictors were considered when $W_i \geq 0.8$. The effect of relevant predictors was determined by model-averaging, *i.e.* calculating the average of estimated coefficients of the 100 models weighted by Akaike weight of each model.

Model validation of the best-fit model (lower AICc) was based on checking the lack of patterns in Pearson and deviance residuals against explanatory variables to assess whether excess of variation is due to a misspecified model. We assessed the lack of overdispersion by verifying that the ratio between the sum of squared Pearson residuals and the difference between the number of observations and the number of regression parameters was about 1 (Zuur et al. 2009). To assess interannual variation, we checked that there were no significant differences in residuals between the two sampling years; therefore, they were considered as replicates. Similarly, to account for spatial correlation, we plotted residuals against latitudinal coordinates and checked for the absence of significant trends. For each selected model, the percentage of explained deviance (D^2) was calculated from the residual deviance (D_r; sum of deviance residuals) and the null deviance (D_0; deviance of the null model) as $D^2 = (D_0 - D_r) / D_0$.

In order to check the role of some biotic factors (*i.e.* competition) in naturalization process, correlation analyses were carried out between Chilean native and exotic species richness. Correlations were done at both regional (considering the 15 sites and two years), and local (considering the 12 quadrats of each site and sampling year) scale.

RESULTS

Considering both countries and growing seasons, a total of 321 species were found. Species richness in Spain was 1.5 times higher than in Chile (Table 3). These differences also occurred at local scale, with a mean of 20.4 (range from 5 to 56) and 14.2 (range from 2 to 25) species/quadrat in Spain and Chile, respectively. Half of the Spanish species were classified as colonizers, that is, they have been described as exotic species in Chile. However, 49 (45%) of these were not found in the Chilean surveys. Native Chilean species represented only half of the species recorded in this country; the other half was formed by exotic species, all of them present in the Spanish flora, although 13 species were not found in our survey in Spain.

Table 3. Numbers of native and exotic species in Chile and exclusive or colonizer species in Spain recorded in the survey plots.

	CHILE		SPAIN	
	Number of species	%	Number of species	%
Native/Exclusive	78	51.3	119	52.0
Exotic/Colonizer	74	48.7	110	48.0
Total	152	100	229	100

Soil and climate relationships

Chile and Spain differed significantly in five of the twelve soil variables, and in five of the six climate variables (Table 4). SOM, S concentration and C/N-ratio were higher in Chilean soils. Texture was also different between countries, being coarser (higher percentage of sand and lower percentage of silt) in Chile than in Spain. For climate variables, only precipitation did not show significant differences between countries.

Table 4. Mean values and range of soil and climate variables in Chile and Spain. Variables with significant differences between countries (t-test, $p \leq 0.05$) are highlighted in bold. Climatic variables were calculated for the 15 sites (n = 15) and soil variables were calculated for the two slope positions per site (n = 30) in each country.

	CHILE		SPAIN		*t*	*p-value*
	Mean	Range	Mean	Range		
Soil variables						
pH	5.7	5.1 – 6.7	5.7	4.8 – 6.6	-0.152	0.880
K (ppm)	154.6	55.1 – 360.9	123.5	54.9 – 260.2	1.445	0.155
Al (ppm)	51.0	20.0 – 109.2	62.2	14.8 – 203.3	-1.001	0.323
B (ppm)	0. 2	0.1 – 0.4	0.2	0.1 – 0.4	1.446	0.154
P (ppm)	3.5	1.4 – 14.5	3.7	0.8 – 10.4	-0.267	0.791
N (ppm)	2.0	0.8 – 4.8	1.8	1.1 – 3.2	1.548	0.129
SOM (%)	4.3	1.02 – 9.2	3.0	1.4 – 6.0	3.501	0.001
S (ppm)	352.8	88.7 – 766.2	202.1	68.4 – 390.8	4.019	0.000
C/N	12.4	5.4 – 16.2	9.8	6.0 – 13.4	5.004	0.000
% Sand	50. 7	23.8 – 82.2	44.1	20.8 – 72.8	2.182	0.033
% Clay	18.7	11.2 – 28.4	19.2	7.6 – 29.6	-0.476	0.636
% Silt	30.6	6.6 – 52.0	36.7	19.6 – 51.4	-2.645	0.011
Climate variables						
PREC[a]	717.7	303-1168	740.8	468-1030	-0.255	0.801
TMED[b]	14.6	13.1-17.0	15.8	14.5-16.9	-3.095	0.005
TMAX[c]	28.2	25.5-30.3	34.01	32.3-35.0	-14.146	0.000
TMIN[d]	4.8	3.1-7.1	3.0	1.3-4.0	4.766	0.000
TOSC[e]	23.3	20.3-26.0	31.0	29.1-32.9	-216.710	0.000
MWD[f]	6.0	4.0-8.0	3.8	3.0-4.0	5.463	0.000

[a)] Annual precipitation; [b)] annual mean temperature; [c)] maximum temperature of the warmest month; [d)] minimum temperatures of the coldest month; [e)] temperature oscillation; [f)] number of months with water deficit

Given the differences in soil and climate variables and in flora components between both countries, the PCA analysis was done for each country separately. The first two components of the soil PCA explained 60.8% and 52.5% of total variance in Chile and Spain, respectively. In the case of Chile, the first soil axis was associated with S, B, N and SOM, whereas the second soil axis was related to pH, Al, P and soil texture. For Spain, the first soil axis was associated with S, N and SOM, whereas the second soil axis was related to pH, Al and B (Table 5). The first two climate components of the PCA explained 87.9% and 81.7% of total variance in Chile and Spain, respectively. In both countries, the first climate axis was associated mainly with precipitation, length of the drought period and maximum temperature, whereas the second climate axis was related to temperature oscillation and minimum temperature (Table 5).

Table 5. Scores of the soil and climate variables in the first two axes of the PCA for Chile and Spain. Variables significantly related to axis coordinates (Pearson correlation, $p \leq 0.05$) are highlighted in bold.

Variable	CHILE		SPAIN	
	Axis 1	Axis 2	Axis 1	Axis 2
Soil variables				
pH	0.154	**0.406**	0.171	**0.455**
K (ppm)	0.339	0.322	0.184	0.118
S (ppm)	**0.381**	-0.082	**0.488**	0.045
Al (ppm)	0.061	**-0.352**	0.068	**-0.531**
B (ppm)	**0.410**	0.073	0.176	**0.451**
P (ppm)	0.234	**0.460**	0.283	0.284
N (ppm)	**0.415**	-0.015	**0.502**	-0.056
SOM (%)	**0.341**	-0.132	**0.493**	-0.210
C/N	-0.151	-0.210	0.291	-0.372
% Sand	-0.276	**0.364**	-0.012	-0.065
% Clay	0.175	**-0.314**	0.056	-0.067
% Silt	0.269	**-0.302**	-0.021	0.131
Eigenvalue	4.874	2.424	3.446	2.849
% Variance	40.6	20.2	28.7	23.7
Climate variables				
PRECa	**-0.905**	0.054	**-0.893**	-0.099
TMEDb	**0.919**	**0.348**	**0.465**	**0.836**
TMAXc	**0.854**	**-0.270**	**0.909**	**0.272**
TMINd	**0.534**	**0.799**	-0.020	**0.993**
TOSCe	**0.347**	**-0.920**	**0.769**	**-0.570**
MWDf	**0.890**	0.033	**0.613**	0.076
Eigenvalue	3.606	1.667	2.922	1.983
% Variance	60.1	27.8	48.7	33.0

[a)]Annual precipitation; [b)] annual mean temperature; [c)] maximum temperature of the warmest month; [d)] minimum temperatures of the coldest month; [e)] temperature oscillation = Tmax-Tmin; [f)] number of months with drought period or water deficit.

According to the validation process, the best models selected for each species group in each country did not show important spatial correlation or interannual variation.

In Spain, the explanatory power of the abiotic variables analyzed was rather limited, as the variance explained by the best model was lower than 19% and 22% for exclusive and colonizer species, respectively. Colonizer species richness was negatively related to CLIM2^2 and SOIL2^2 (Table 6), being higher at intermediate values of TMIN, TOSC and pH, Al and B, while exclusive species richness was positively associated to lower slope zones (Fig. 16).

Table 6. Parameters and unconditional sampling variances (U. var.) for the nine predictors obtained considering the 100 better models of native/exotic species in Chile and colonizer/exclusive species in Spain. Relevant predictors (relative importance, Wi ≥ 0.8) are highlighted in bold. CLIM and SOIL correspond to the components of the respective PCA, whereas 1 or 2 indicate the axis of the PCA. ^2 represent the quadratic term. The predictor SLOPE is the slope position.

	CHILE				SPAIN			
	Natives		Exotics		Exclusives		Colonizers	
	Parameter	U. variance	Parameter	U. variance	Parameter	U. variance	Parameter	U. variance
CLIM1	0.0702	0.00470	**-0.0981**	0.00201	0.0109	0.00051	-0.0048	0.00014
CLIM2	-0.0176	0.00124	**0.2970**	0.00260	0.0715	0.00455	-0.0027	0.00009
CLIM1^2	-0.0809	0.00383	-0.0371	0.00211	-0.0147	0.00061	0.0206	0.00059
CLIM2^2	**-0.1290**	0.00147	**-0.1260**	0.00106	-0.0239	0.00114	**-0.0410**	0.00078
SOIL1	**0.0522**	0.00074	-0.0055	0.00011	-0.0218	0.00074	0.0056	0.00011
SOIL2	**0.1280**	0.00142	0.0107	0.00035	0.0039	0.00009	0.0025	0.00004
SOIL1^2	-0.00004	0.000004	0.00003	0.000002	-0.00016	0.000002	-0.0044	0.00004
SOIL2^2	-0.0245	0.00038	-0.0165	0.00021	0.0047	0.00007	**-0.0147**	0.00011
SLOPE			-0.0034	0.00034	**0.1820**	0.00477	0.0180	0.00104

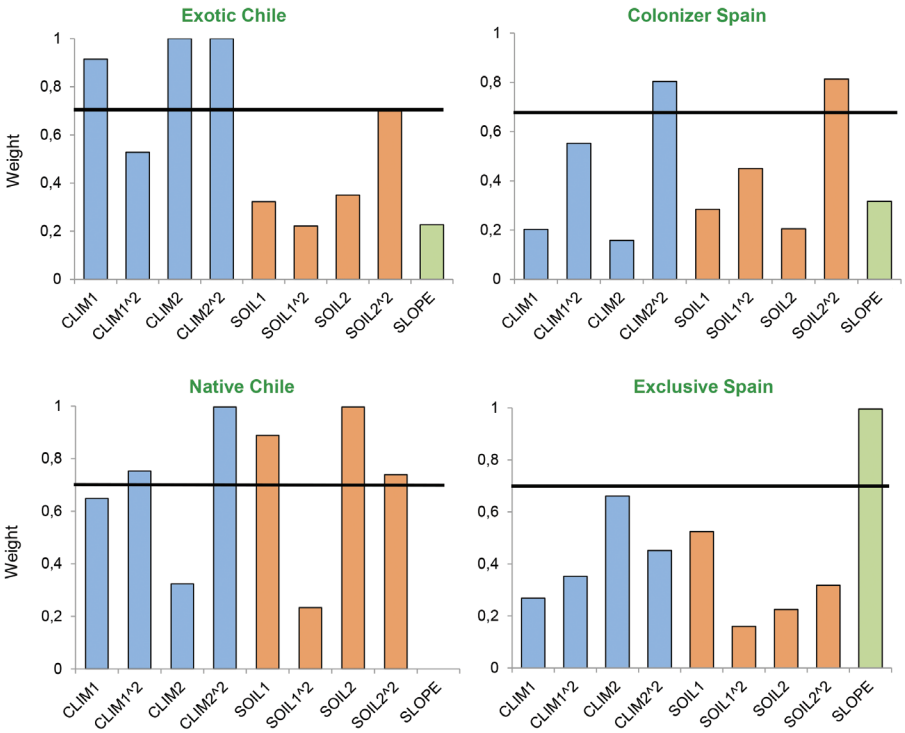

Fig. 16 Relative importance of each predictor (W_i) according to Akaike weights. Blue bars represent climate predictors (CLIM1, CLIM2, CLIM1^2, CLIM2^2), salmon bars represent soil predictors (SOIL1, SOIL2, SOIL1^2 and SOIL2^2) and green bar represents the geomorphologic predictor, the slope zone (SLOPE). Discontinuous lines denote relevant predictors in each situation ($W_i \geq 0.8$)

In Chile, the explanatory power of the best model on species richness was below 40% for natives and 75% for exotic species. Climate had an effect on both native and exotic species while soil characteristics only influenced natives (Fig. 16). Native species richness was negatively related with CLIM2^2, and positively related with SOIL1 and SOIL2 (Table 6), therefore it can be expected to be higher in areas with coarser soil texture, higher pH and soil fertility, and at intermediate values of TMIN and TOSC. Exotic species richness was negatively related with CLIM1 and had a hump-shaped response with CLIM2; then, number of exotic species increased monotonically with precipitation and had an unimodal response with TOSC and TMIN, raising the highest richness at intermediate values of both variables. As an example, annual precipitation, the main variable representative of the first climate axis, was positively correlated with plant species richness in Chile (Fig. 17). The relationship was significant for the number of exotic species ($r = 0.652, p \leq 0.001$), but not for native ones.

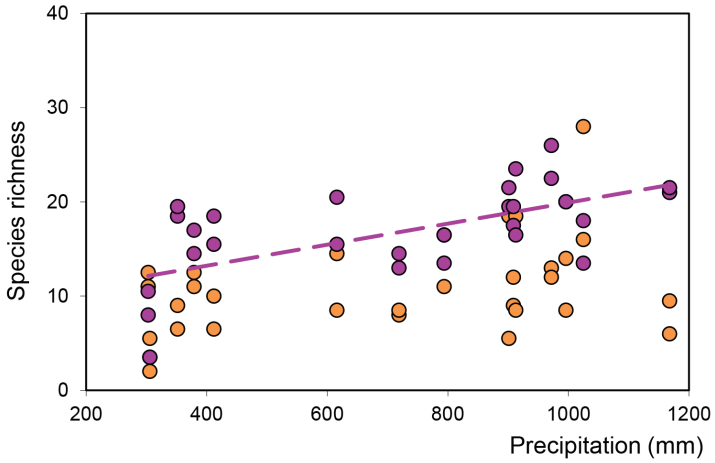

Fig. 17 Relationship between species richness and annual precipitation in sampled plots of Chile. Purple circles and purple discontinuous lines represent exotic species, and orange circles represent native species. Only significant relationships are shown ($p \leq 0.05$)

Native vs exotic species richness

At regional scale, native and exotic species richness was not significantly correlated in Chilean sites (r=0.124, p = 0.514; Fig. 18a). Considering the 30 correlations conducted by site and year, only three were significantly positive and seven were significantly negative. Although most of those local correlations were non-significant, results showed a trend towards positive correlations at sites with lower total species richness, and negative correlations when total species richness was higher (Fig. 18b).

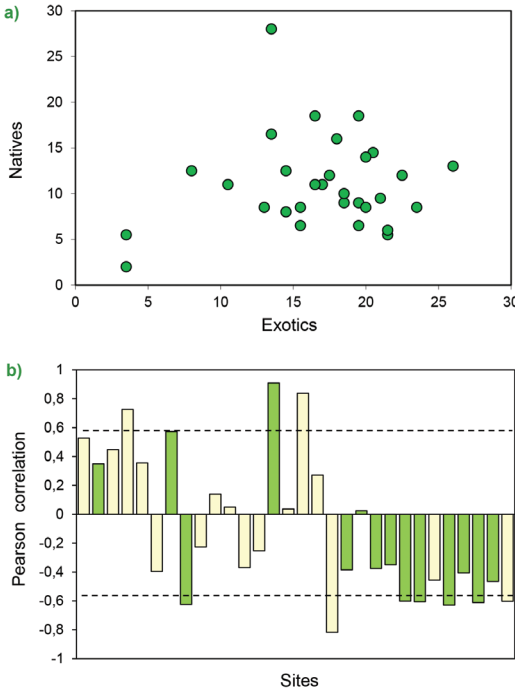

Fig. 18 (a) Relationship between native and exotic species richness in Chile considering 15 sites and two years. (b) Histogram showing Pearson correlation coefficients (positive or negative) between exotic and native species richness in Chile at each of the fifteen sites in the two sampling years (2010: light yellow, 2011: green bars). Discontinuous lines denote significant correlation value ($p \leq 0.05$). Sites are ordered by total species richness

DISCUSSION

Mediterranean-type ecosystems around the world present a great opportunity to compare and understand the mechanisms determining the success of introduced species within a region (Groves and Di Castri 1991; Pauchard et al. 2004). This is especially important in the case of the Mediterranean regions of America and Spain due to their long history of species exchanges. The *espinal* in Chile and the *dehesa* in Spain present great similarities in terms of climate, lithology, plant physiognomy and land use. Their herbaceous vegetation also shares an important number of species because the origin of the exotic species naturalized in central Chile region is almost exclusively the Mediterranean Basin, and mainly Spain (Groves, 1986). In addition, the present study includes a wide range of Mediterranean-type climates in both countries but with similar lithology. These commonalities between the two regions provide an excellent scenario to analyze the importance of biotic and abiotic factors in the arrival and establishment of exotic species in Chile (Jiménez et al. 2008). The results of this study indicate that exotic species richness in Central Chile is a complex process driven by successive selective filters acting at the source (limiting the number of donor species) but mainly at the recipient area (conditioning the naturalization process).

In the source area (Spain), species richness is higher than in Chile. This finding may be related to its lower soil fertility (an inverse relationship between species richness and fertility has been described in Mediterranean-climate regions (Huston 1994; Holmgren et al. 2000)), as well as a shorter land-use history. The high species richness characteristic of grasslands in the Mediterranean Basin has been related to their millenary agrarian use (Perevolotsky and Seligman 1998), which has favored the co-evolution of plants with agrarian activities (Cowling et al. 1996; Hille Ris Lambers et al. 2010). On the one hand, the number of Chilean native herbaceous species is low, possibly related to the evolution of its flora in a region with scarce incidence of natural fire regimes (Aschmann and Bahre 1977; Aravena et al. 2003) and other disturbances until European arrival (Arroyo et al. 1995). On the other hand, drastic landscape transformation by humans over the last centuries not only reduced native flora but could also create opportunity windows (Shea and Chesson 2002) for exotic plants to colonize the Chilean *espinal*.

Although the number of exotic species recorded in Chile is high, it represents a small fraction (32%) of all the Spanish species recorded in our study, or even of those Spanish species that have already become naturalized in Chile (45% of colonizer species). Nonetheless, sampling in both Chile and Spain was conducted over a wide range of environmental conditions, hence this result seems to indicate that some kind of filter has acted selectively on species between the source and the recipient area: they did not get to leave Spain, failed in transport pathway or failed to establish in Chile. The first two steps are difficult to know due to limitations of this type of studies (Kolar and Lodge 2001). As for establishment failure, Castro et al. (2005) estimated that between 7,070 and 35,400 exotic species were capable of reaching Chile as a consequence of the massive invasion of plant species to South America during the last five centuries, but less than 10% (assuming the tens rule of Williamson (1996)) are currently naturalized. The fact that many of the Spanish species classified as colonizer (and therefore present in Chile) have not appeared in our survey points out to failures in the establishment associated with abiotic filters. This explanation agrees with the existence of soil and climate predictors for colonizer species richness, but not for exclusive ones. In Spain, those species able to arrive and establish in Chile (classified as colonizer) are more dependent on environmental conditions than those that could not (classified as exclusive), or, in other words, the species able to arrive and establish in Chile are those more dependent on environmental conditions in the source area.

Once in the recipient area, abiotic rather than biotic filters mainly determine the establishment success of exotic species in Chile. Chilean native species richness has weak but significant and positive relationships with edaphic conditions, like soil fertility, texture and pH. Nevertheless, exotic species richness has strong significant relationships with climate, increasing species richness when precipitation increases and summer drought period becomes shorter. This could be interpreted as different environmental filters acting in each group of species (edaphic for natives, climatic for exotics). Previous studies show that in semi-arid ecosystems, increase in water availability may promote colonization processes (Cleland et al. 2004; Kreyling et al. 2008); in our study, increase in precipitation favors exotic species, suggesting that wetter Mediterranean areas are more prone to the establishment of exotic species. Therefore, it could be important to identify wetter sites in Central Chile that might be more susceptible to colonization.

Regions with similar macroclimates may have specific habitats linked to subtle differences in geography, topography, microclimate or in land-use history (Pauchard et al. 2004). For instance, the longer summer drought period in Chile compared to Spain is related to the lower latitude of the Mediterranean Chilean region and the fact that precipitation occurs mainly in winter (Aschmann 1973) instead of being in autumn and spring, as it occurs in Spain (Font Tullot 2000). The longer period of drought in Chile also acts as an environmental filter limiting the number of naturalized species, especially in drier Mediterranean areas where water deficit in summer could extend for up to 8 months. In fact, several of the colonizer species not found in the *espinal* survey are mainly (*e.g*, *Agrostis castellana, Phleum pratense* or *Trifolium arvense*) or exclusively (*e.g. Bromus tectorum, Papaver dubium, Poa bulbosa* or *Stachys arvensis*) present in Chile at higher latitudes (see http://www.lib.udec.cl/database.html for species distribution area) with a wetter and cooler climate and a shorter drought period. This latitudinal displacement is possibly due to the longer duration of growing period in the donor area and it is in line with the trend of increasing exotic species richness as precipitation increases. This supports the increased resource availability hypothesis (Davis et al. 2000; Richardson and Pyšek 2006), being colonization promoted by an improvement in the main limiting resource (Cleland et al. 2004; Kreyling et al. 2008). Water availability appears to be the main limiting resource constituting an important factor determining species richness in semi-arid environments, as occurs in California (Richerson and Lum 1980), and therefore its increase favors colonization (Thomsen et al. 2006).

The accepted idea that naturalization of exotic species decreases native biodiversity (Richardson et al. 1989; Davis 2003) has been debated during the last decade (Houlahan and Findlay 2004; Richardson et al. 2007). In terms of species richness, our results agree with most recent studies (Gaertner et al. 2009; Jiménez et al. 2011) showing that there is an effective coexistence between native and exotic species in Chile. Many authors have considered that the existence of negative correlations between native and exotic species richness at local level is a sign of competition (Cleland et al. 2004; Bartomeus et al. 2012). At regional scale, the relationship between native and exotic species is not significant **(Fig. 18a)**, corroborating the different influence of climate and soil characteristics on both species groups. When sites and years are considered separately most of the relationships are also non-significant **(Fig. 18b)**, suggesting that native have not been excluded by exotics species through competition. Although only few significant relationships were found, our results show that sites with higher species richness tend to have negative relationship (competition) between natives and exotics. This result agrees with Gilbert and Lechowicz (2005), who suggested that among other factors, non-saturation of species in plant communities could be the mechanism of co-existence between native and exotic species. Thus, it seems that plant competition is not an important biotic filter for the naturalization process in the Chilean *espinal* since 1) the lack of significant native-exotic species correlations at local scale, and 2) most of species studied are annuals

(75% of the 152 species considered in Chile), therefore, their life span limits the possibilities of competition for space to short periods of time and they have to start over interspecific relationships each year (supported by interannual differences obtained in correlations showed in Fig. 18b).

In summary, exotic flora in central Chile is the result of a filtering process driven mainly by abiotic factors. The first filter acts on the ability of the Spanish species to reach Chile, limiting the number of colonizers that arrived to and established in the study area. Therefore, an abiotic filter is acting in the source area (climatic conditions are related to the number of colonizers but not exclusives), although it also could be related to land-use or characteristics of the species, both of which are beyond the scope of this work. Once in the recipient area, an abiotic filter is acting again, with exotic species richness being positively related to water availability as the limiting factor. Even that these abiotic filters influence the naturalization process, it seems that exclusion due to competitive relationships between native and exotic species have no influence on it, possibly related with the low native species richness. Finally, all these filtering processes allow for the coexistence of native and exotic herbaceous species in Chilean Mediterranean grasslands.

Naturalización transcontinental de especies herbáceas en pastizales mediterráneos españoles y chilenos

Transcontinental naturalization of herbaceous species in Spanish and Chilean Mediterranean grasslands

Chapter 4 Community structuring

"Nothing is perfect. Life is messy. Relationships are complex. Outcomes are uncertain. People are irrational"

Hugh Mackay

Adapted from: de Miguel JM, Martín-Forés I, Acosta-Gallo B, del Pozo A, Ovalle C, Sánchez-Jardón L, Castro I, Casado MA Non-random co-occurrence of native and non-native plant species in Mediterranean pastures. Acta Oecologica (in review)

INTRODUCTION

Community assembly is a relevant issue in ecology from a theoretical (Hillebrand and Matthiessen 2009; HilleRisLambers et al. 2012; Pysek and Chytrý 2014) and applied point of view (Young et al. 2001). Most of the studies of species co-occurrence have focussed on the importance of abiotic and biotic factors acting on the species present in a given region (Diamond 1975; Chase 2003; Götzenberger et al. 2011). However, other studies highlighted the importance of evolutionary and biogeographical processes on the configuration and composition of the regional species pool (Ricklefs 2004; HilleRisLambers 2012), which can even be more important than local filters (Chase 2003; Zobel and Partel 2008). This regional pool is in many cases a mixture of species of different evolutionary origin (Harrison and Grace 2007), particularly in regions with high levels of plant invasion.

Processes of biological invasion represent excellent scenarios for analyzing patterns of communities' organization and assembly. The degree of successful establishment of exotic species depends upon their adaptation to the new environmental conditions and on their interaction with other species with which they had not previously co-existed. This interaction gives rise to a reorganization in the assembly of species, which will likely be seen in changes in their spatial patterns. Comparison of these patterns with those existing in the region of origin of the exotic species can provide valuable information on the role played by these species in structuring communities. This kind of study is uncommon despite the fact that coexistence of species from different biogeographic origins has been recognized as an interesting case of community assembly (Davis et al. 2011; Dostál 2011; Sutherland et al. 2013).

Grasslands in different Mediterranean climates share a large amount of species, most of them being natives from the Mediterranean Basin but exotics elsewhere (Arianoutsou et al. 2013). Several studies have shown the high values of plant richness they maintain (Pineda and Montalvo 1995; Cowling et al. 1999; Ovalle et al. 2006; Maltez-Mouro et al. 2010). There has been little research, however, into the influence of the invasion process on the spatial organization of these plant communities despite the fact that some studies recognize the importance of the assembly history in the structure of these communities (Sanders et al. 2003; Martin and Wilsey 2012). After an invasion process, the community assembly is driven by the action of different abiotic and biotic factors (Gutiérrez et al. 2014): interspecific competition, toleration, or facilitation (Diamond 1975; Madrigal et al. 2011), environmental inter-regional differences and habitat histories (Holmgren et al. 2000; Pauchard et al. 2004; Arianoutsou et al. 2013), as well as by the regional species pool, particularly the biogeographical origin and history of arrival of its components (Figueroa et al. 2004; Castro et al. 2005). These factors might have conditioned the assembly of introduced species and the latter together with the native ones in Mediterranean grasslands outside Europe, which is displayed in the degree of their spatial organization (pattern co-occurrence).

In the present paper we analyze the spatial patterns of herbaceous species co-occurrence in grasslands in two Mediterranean regions (Spain and central Chile) subjected to similar cultural regimes within a silvopastoral system. In Chile, the invasion process is associated with the introduction of European agriculture in the XVI century (Groves and Di Castri 1991; Arroyo et al. 1995). More than 500 species of exotic plants, mostly from the Mediterranean Basin, have been reported for central Chile (Figueroa et al. 2011; Martín-Forés et al. 2012), which represent 18% of the flora in this region. If only Chilean seminatural grasslands are considered, this figure surpasses 40% (Martín-Forés et al. 2012). The time of residence of herbaceous species introduced into Chile varies greatly (Castro et al. 2005) and their early distribution possibly followed a random pattern, more associated to the introduction of agrarian activities than environmental factors driving the distribution of species (Groves and Di Castri 1991; Figueroa et al. 2004; Castro et al. 2005; Wilson et al. 2009; Fuentes et al. 2013).

The aim of this study is to identify inter-regional differences in the spatial organization (*i.e*. species co-occurence) of native and non-native species. We hypothesize that: i) in a similar environmental and cultural context, the colonizer species can reach the same degree of spatial organization in both regions, and ii) as a result of a possible disassembly of the invaded Chilean communities, the degree of spatial organization of the colonizers in Chile might be higher than that of the Chilean exclusive species. We study 15 sites in each country distributed throughout an extensive territory and sampled during two consecutive years. We identify the species spatial organization patterns in both regions by means of null models for three groups of species: the Spanish ones introduced in Chile (colonizers), those with exclusive presence in each region (exclusives) and both groups considered together. The potential underlying mechanisms of the patterns identified are examined.

MATERIAL AND METHODS

Study area

The study was conducted in the Chilean *espinal* and the Spanish *dehesa*, two silvopastoral systems used for extensive livestock grazing in Mediterranean grassland areas. Both ecosystems are very similar in terms of physiognomy, livestock, management technology and the associated cultures (Ovalle et al.1996; Marañón 1988). They differ with regard to their woody vegetation but are very similar in the structure of the herbaceous vegetation. The *dehesa* contains scattered trees of holm oak (*Quercus ilex* subsp. *ballota* (Desf.) Samp.) or cork oak (*Quercus suber* L.) within a herbaceous matrix mainly comprising winter annuals (Joffre et al. 1999; Marañón et al. 2009). Its origin dates back several centuries or millennia, when human intervention in woodlands transformed the landscape into a pseudosavannah (Le Houérou 1981; López et al. 2007). On the other hand, the *espinal* represents a recent and largely anthropogenic formation (Ovalle et al. 1999) associated with the transformation of the landscape following the Spanish colonization in the 16th century (Arroyo et al. 2000; Figueroa et al. 2004). It is covered with dispersed trees of *Acacia caven* Mol. (known as *espino*) within a herbaceous matrix mainly comprising annual plants, native and exotic species of Mediterranean origin (Ovalle et al. 1996, 2006; del Pozo et al. 2006). The *dehesa* represents the source area for most of the Chilean exotic species of the *espinal*, and therefore constitutes an excellent scenario for studying the process of colonization and naturalization of exotic species (Pauchard et al. 2004; Jiménez et al. 2008; Martín-Forés et al. 2012).

In Chile we selected an area comprising 600 km from 32°35’ to 37°00’ S and from 70°46’ to 72°35’ W. In Spain the investigation was conducted in the center-west of the Iberian Peninsula, from 40°13’ N to 37°51’ N and from 4°23’ W to 7°02’ W (Fig. 19). The two study areas covered a wide range of climate conditions in which *dehesas* and *espinales* are distributed. Mean annual temperature ranged from 13.1 to 17.0ºC and from 14.5 to 16.9ºC in Chile and Spain respectively, whereas annual precipitation varied from 303 to 1168 mm and from 468 to 1030 mm, respectively. Soils in both regions were slightly acidic, derived from igneous or metamorphic rocks and the topography was hilly.

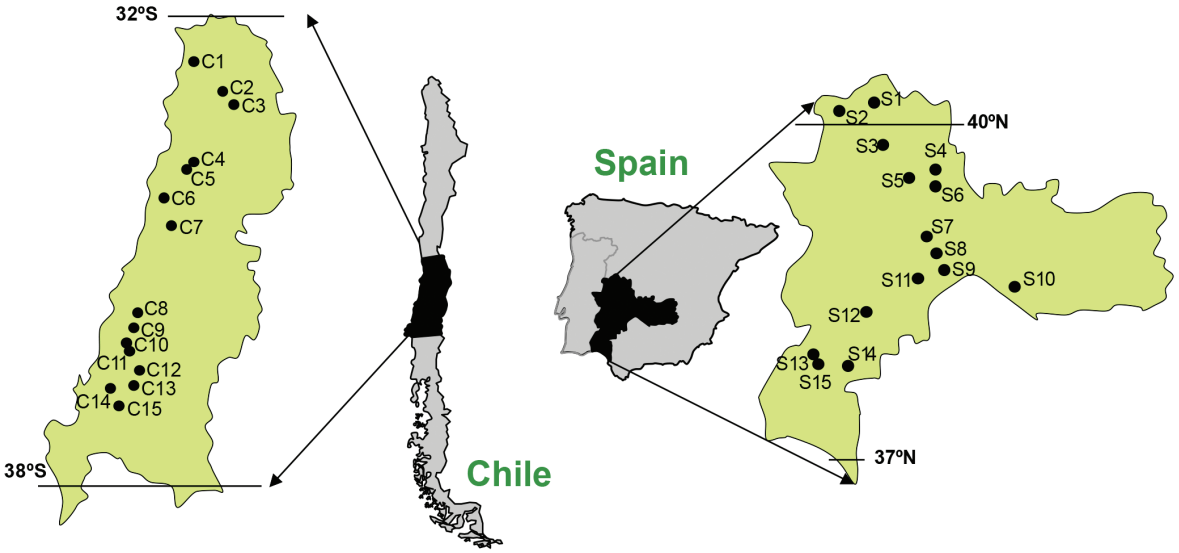

Fig. 19 Location of the sites of Mediterranean grasslands in Spain and Chile considered in the present study. See Table 7 for codes and species richness of each site

Data collection

We selected fifteen sites in each country in order to cover the whole range of environmental conditions in which the *dehesas* and *espinales* are distributed. In each site, two 10 x 10 m plots, separated by at least 40 m, were selected. In each plot, six 50 x 50 cm quadrats were randomly distributed and the presence of all the herbaceous species existing within each quadrat was assessed. In order to avoid the influence of trees (holm oaks or *espinos*), we always situated the quadrats in open areas (Marañón et al. 2009; De Miguel et al. 2013). As most of the herbaceous plant species in Mediterranean-type ecosystems display some inter-annual composition variability (Peco et al. 1983; Figueroa and Davy 1991), sampling was conducted during two consecutive growing seasons (2010 and 2011). The Chilean species were classified as native or exotic, according to Marticorena and Quezada (1985, 1987) and Fuentes et al. (2013). All the Chilean exotic species recorded in samples were common to the Spanish *dehesas*. In the case of Spain, all the species were native and were classified as colonizers (the ones that have become naturalized in Chile) or exclusives (only present in Spain).

We performed analyses for three groups of species in each country: exclusives (natives that appeared only in one of those countries), colonizer (the Spanish ones introduced in Chile), and both groups together ('all species'). Plant species richness (total number of species), number of colonizer and exclusive species in Chile and in Spain were calculated for each site and growing season (Table 7).

Table 7. Codes (see Fig. 19), geographical coordinate, and richness of herbaceous species of the 15 sites sampled in each country.

					Herbaceous plant richness					
					All species		Colonizer species		Exclusive species	
	Site	Code	Latitude	Longitude	2010	2011	2010	2011	2010	2011
	Catapilco	C1	32°35'52''S	71°18'50''W	34	37	24	24	10	13
	Liaillay	C2	33°00'25''S	70°53'41''W	21	30	8	14	13	16
	Colina	C3	33°07'47''S	70°46'34''W	13	9	6	5	7	4
	Melipilla	C4	33°49'18''S	71°18'51''W	31	33	21	21	10	12
	San Pedro	C5	33°55'08''S	71°26'24''W	32	39	20	21	12	18
	Alcones	C6	34°18'56''S	71°44'21''W	43	47	25	28	18	19
	Pumanque	C7	34°37'46''S	71°42'53''W	28	35	16	20	12	15
CHILE	La Estrella	C8	35°46'46''S	72°11'47''W	43	56	24	33	19	23
	Cauquenes	C9	35°58'49''S	72°13'36''W	40	49	17	23	23	26
	Quirihue 1	C10	36°10'18''S	72°27'08''W	35	44	22	24	113	20
	Quirihue 2	C11	36°15'21''S	72°32'54''W	49	51	29	31	20	20
	San Nicolás	C12	36°29'20''S	72°13'20''W	44	53	26	27	18	26
	Rucapequen	C13	36°40'22''S	72°15'09''W	44	43	27	28	17	15
	Larqui	C14	36°42'32''S	72°15'51''W	55	52	21	22	34	30
	Yumbel	C15	37°00'23''S	72°33'55''W	40	41	29	30	11	11
	Bronco	S1	40°12'59''N	6°20'39''W	64	76	37	48	26	28
	Cilleros	S2	40°06'58''N	6°45'24''W	57	68	43	48	13	19
	Serradilla	S3	39°45'41''N	6°06'56''W	73	74	48	45	24	29
	Navalvillar de Ibor	S4	39°32'53''N	5°22'57''W	43	55	25	34	18	20
	Madroñera	S5	39°25'21''N	5°47'43''W	60	65	38	47	21	17
	Logrosán	S6	39°21'28''N	5°25'03''W	53	58	36	41	16	17
	Casas de Don Pedro	S7	39°05'57''N	5°19'26''W	77	57	50	37	26	20
SPAIN	Puebla de Alcocer	S8	38°57'15''N	5°13'18''W	64	50	39	31	25	19
	Cabeza de Buey	S9	38°46'38''N	5°12'43''W	70	68	47	43	23	25
	Alcudia	S10	38°36'49''N	4°23'25''W	52	56	38	37	13	19
	Castuera	S11	38°46'20''N	5°34'47''W	72	48	37	28	35	20
	Fuente del Canto	S12	38°16'33''N	6°20'21''W	66	71	42	42	23	28
	Aroche	S13	37°58'01''N	7°01'26''W	53	51	37	35	15	15
	Aracena	S14	37°51'58''N	6°33'52''W	81	69	47	47	33	21
	Cortegana	S15	37°56'21''N	6°51'52''W	75	62	44	39	30	22

Data analyses

We used null models to analyze patterns of species co-occurrence (Gotelli and McCabe 2002). Despite the constant debate (Ulrich and Gotelli 2013; Veech 2013), null models constitute a sound option for comparing the spatial structure of communities in areas presenting different environmental conditions (Gotelli and Graves 1996; Weither and Keddy 1999; Gotelli 2000). These models involve statistical tests based upon randomization of ecological data generating random community patterns, and have been used to detect patterns in binary species presence-absence matrices (Gotelli

2000; Álvarez-Pérez and Herrera 2013; Ulrich and Gotelli 2013). Comparison of random patterns with those observed in the communities analyzed provides information on the mechanisms (biotic interactions and abiotic filters) structuring communities. For a structured community, the observed co-occurrence of species should be significantly different (higher or lower depending upon the co-occurrence index employed) from the random co-occurrence pattern.

We analyzed the differences between the observed and random co-occurrence pattern in Spain and Chile for the two sampling years (2010 and 2011) and for three sets of species: colonizer ones, exclusive ones and the set of 'all species'. For each country and year we organized the data into presence-absence matrices in which each row represented the species of each set and the columns showed the 15 sites sampled.

The species co-occurrence patterns were analyzed using two indices provided by EcoSim 7.0 simulation software (Gotelli and Enstminger 2012) and which are commonly used as indices of co-occurrence: the number of Checkerboard species pairs (Diamond 1975; Gotelli and McCabe 2002) and the C-score index (Stone and Roberts 1990). The number of Checkerboard species pairs (Checkerboard index) is calculated by counting the number of unique pairs of species never co-occurring. It is a very strict index of the degree of co-occurrence, because it requires perfect segregation of the species. In a structured community (*e.g.* as a result of strong competitive interactions between species), there should be a significantly greater amount of species pairs that never co-occur (perfect checkerboard distribution) than to what might be expected randomly. The C-score index quantifies the average number of 'checkerboard units' (CU) between all possible pairs of species. A checkerboard unit is any submatrix of the form: 10/01 or 01/10. For any given pair of species, CU is calculated as: $CU = (R_i\text{-}S)\ (R_j\text{-}S)$, R_i and R_j being the number of presences for species i and species j, respectively, and S the number of sites occupied by both species (Gotelli and Entsminger 2012). This index also measures the degree to which species not co-occur across a set of sites but it is not as stringent as the Checkerboard index because it does not require complete segregation (Gotelli and McCabe 2002). In a structured community the observed C-score value should be significantly higher than expected by random.

We compared the observed values of both indices with the distribution of the expected values obtained from 5,000 matrices generated randomly by EcoSim software. A null model algorithm with a low risk of Type I error (FF= Fixed-Fixed) was selected (Gotelli 2000; Gotelli and Enstminger 2012). In FF algorithm, both the sum of the rows (species) and the sum of the columns (sites) remain constant in the simulated matrices. This algorithm leads to the assumption that the probability of a site being colonized is proportional to the species richness it harbours, and it therefore adjusts to the environmental reality imposed by each site.

EcoSim provides for each of the two indices selected the observed, expected by random, and standardized effect size (SES) values, which provides information on the number of standard deviations that the observed index is above or below the mean index of the simulated communities (Gotelli and McCabe 2002). The SES values are comparable among different datasets. Either positive or negative SES values show a spatial segregation of species, greater or lower, respectively, than that expected from random. Absolute SES values show the degree of that spatial segregation. For each index EcoSim provides the *p-values*, which inform about the statistically significant difference of the values observed in relation to those obtained from the 5,000 simulations (Gotelli and Enstminger 2012).

RESULTS

The observed values and those randomly obtained for the Checkerboard and C-score indices are shown in Tables 8 and 9, respectively. In general terms, the inter-annual differences between the values observed and the SES values (Fig. 20) of both indices were smaller than inter-regional ones.

Table 8. Analyses of species co-occurrence in Chile and Spain using the Checkerboard index for different groups of species and Fixed-Fixed null model algorithm. The asterisk in significant *p-values* indicates observed checkerboard values lower than simulated ones. NS non-significant *p-values* ($p > 0.05$).

		Simulated Checkerboard		
	Observed Checkerboard	**Mean**	**Variance**	**p-value**
All species				
Chile 2010	3538	3406.2	2104.2	0.0020
Chile 2011	3713	3594.8	1885.9	0.0020
Spain 2010	9697	9343.5	3104.3	<0.0001
Spain 2011	6767	6584.0	2057.9	<0.0001
Colonizer species				
Chile 2010	656	620.87	234.9	0.0100
Chile 2011	913	841.04	268.3	<0.0001
Spain 2010	1450	1374.38	512.8	<0.0001
Spain 2011	1048	1013.46	445.4	NS
Exclusive species				
Chile 2010	1013	986.41	345.5	NS
Chile 2011	862	900.36	364.8	0.0206*
Spain 2010	3488	3402.37	555.4	<0.0001
Spain 2011	2365	2290.16	279.7	<0.0001

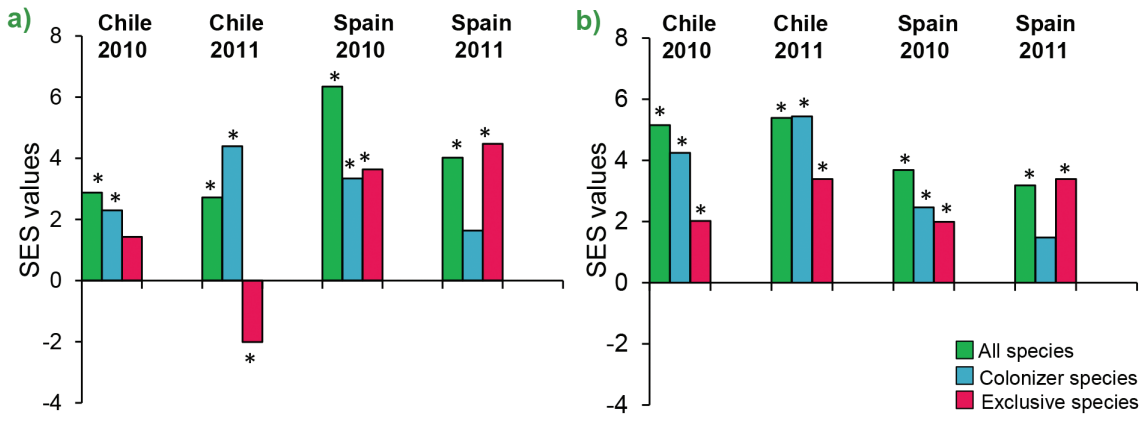

Fig. 20 Standardized effect size (SES) values for analyses of co-occurrence of three groups of grassland species for Chile and Spain in 2010 and 2011, using the Checkerboard index (a) or the C-score index (b) for Fixed-Fixed null model algorithm. The asterisk represents significant differences ($p < 0.05$) between observed and simulated values

Table 9. Analyses of species co-occurrence in Chile and Spain using the C-score index for different groups of species and Fixed-Fixed null model algorithm. NS: non-significant *p-values* ($p > 0.05$).

		Simulated C-score		
	Observed C-score	Mean	Variance	p-value
All species				
Chile 2010	4.72	4.61	0.0004	<0.0001
Chile 2011	4.82	4.71	0.0004	<0.0001
Spain 2010	4.53	4.47	0.0002	<0.0001
Spain 2011	5.09	5.05	0.0001	0.0004
Colonizer species				
Chile 2010	4.85	4.72	0.0009	<0.0001
Chile 2011	4.79	4.65	0.0007	<0.0001
Spain 2010	5.27	5.22	0.0004	0.0162
Spain 2011	5.72	5.69	0.0003	NS
Exclusive species				
Chile 2010	4.13	4.04	0.0022	0.0346
Chile 2011	4.60	4.45	0.0018	<0.0001
Spain 2010	3.78	3.73	0.0007	0.0328
Spain 2011	4.38	4.31	0.0004	<0.0001

The SES values of Checkerboard and C-Score in Spain and Chile were mostly positive and significantly different from random, indicating a spatial segregation higher than the expected from random (Fig. 20). The only negative SES value was the Checkerboard for exclusive species in Chile in 2011. Nonetheless, we detected clear inter-regional differences between both indices, depending upon the groups of species considered. The species exclusive to Spain exhibited absolute SES values higher than the exclusive species of Chile for the Checkerboard index (Fig. 20a), and very similar ones for the C-Score index (Fig. 20b). The colonizer species in Chile reached SES values for the C-Score index much higher than those recorded for the same species in Spain, and in both years they were significantly different from random (Fig. 20b). However, when considering the Checkerboard index, the inter-regional difference for colonizers was not so clear, although the highest and lowest absolute SES values were reached in Chile (2011) and in Spain (2011) respectively (Fig. 20a). For the group 'all species' the results differed depending upon the indices considered. The SES values for the Checkerboard index were always positive and significantly different from random in both countries, although they were higher in Spain than in Chile in the two years analyzed (Fig. 20a). For the C-Score index the SES values were equally positive and different from random in both countries, but in this case, they were higher in Chile in the two years considered (Fig. 20b).

DISCUSSION

In our study, in most cases, the segregation of species is higher than the expected from random (positive SES values), showing structured communities. This pattern is expressed with different intensity in Spain and Chile and between the two years considered. The temporal variation is possibly related to the dynamics of inter-annual floristic composition characteristic of Mediterranean grasslands communities, which are dominated by annual species (Peco et al. 1983; Figueroa and Davy 1991). However, the differences encountered between the two years are of scarce magnitude compared with those existing between both countries, which indicates greater geographic than temporal variability. The community assembly process is driven by the action of different abiotic and biotic filters, thus, those factors could be acting in the spatial segregation of species. A high degree of spatial segregation tends to be attributed to groups of species with different environmental requirements, or to intense interspecific competition associated with the scarce contribution of toleration and facilitation mechanisms (Diamond 1975; Connor and Simberlof 1979; Gotelli and Graves 1996; Weither and Keddy 1999; Götzenberger et al. 2011). Although we did not explore the causes of species co-occurrence, the result obtained is coherent with a strong influence of abiotic factors upon species distribution (Peres-Neto 2004; McCreadie and Bedwell 2013; Martín-Forés et al. 2015). At a broad geographical scale (inter-sites), as considered in our study, some authors report that the environmental heterogeneity seems to determine spatial segregation whereas at plot scale, the spatial segregation seems to be influenced by species interactions (Reitalu et al. 2008). The conditions imposed by the environmental heterogeneity (*e.g.* edaphic conditions, and rainfall and temperature variability associated with the environmental gradient analyzed within each country) determine the absence of certain species in determined sites, as they are not well adapted to these environments. When the scenario simulated contemplates the above-mentioned limitations (FF algorithm), the results obtained indicate that species respond to the environmental heterogeneity becoming better organized therein than what might be expected from random. The influence of biotic factors, however, cannot be ruled out in this result, as this kind of factors might also be conditioning the observed co-occurrence values. Whether biotic factors acted, the results would have indicated a preponderance of interspecific competition instead of tolerance and/or facilitation in the grasslands communities' assembly in both countries. There is a need for further study to clarify these hypotheses.

The inter-regional differences revealed by the co-occurrence indices depend upon the group of species analyzed. For the group of 'all species', SES values for the Cherckerboard index indicate a clearer spatial segregation of the species in Spain than in Chile. Nonetheless, on considering the values of the C-Score index, the values observed in both regions are also significantly higher than the expected from random, although in this case the difference from random is greater in Chile than in Spain. Although the C-Score index is not as demanding as the Cherckerboard index as a measure of the degree of co-occurrence, (Gotelli and McCabe 2002), this discrepancy between indices does not allow confirming clear inter-regional differences when considering all species together.

The results obtained for the group of 'all species' can be accounted for by the different roles played by the colonizer species and the exclusive ones detected in both countries. The species exclusive to Spain maintain a clearer spatial segregation than Chile's exclusive ones. However, the colonizer species in Chile exhibit a clearer spatial segregation than in Spain. The latter result indicates that the time since the arrival of the Spanish colonizer species to Chile has been sufficient to reach a non-random spatial segregation, establishing structured communities of these species, even more clearly than in their region of origin. This fact does not fully coincide with the hypothesis of our study. In the grasslands of Chile's Mediterranean region, the Spanish colonizer

species might be exposed to greater competition possibly due to their coexistence with native species, or due to the higher environmental heterogeneity that favor habitat preferences more than in their own region of origin (Connor and Simberlof 1979; Gotelli and Graves 1996; Weither and Keddy 1999). In our study, the role of environmental heterogeneity as the main factor to explain the latter is supported by the fact that the climate gradient in Chile is broader than that in Spain, with wider ranges of temperature and precipitation and longer summer drought periods (Martín-Forés et al. 2015).

Both exclusive Spanish species and colonizers in Chile show a greater degree of spatial segregation than exclusive Chilean species, which confirms the first hypothesis of our study. The introduction of a European agricultural system in Chile's Mediterranean region involved the establishment of disturbance regimes heretofore unknown in this region, such as periodic plowing, a high livestock load and fire (Muñoz and Fuentes 1989). These conditions not only favored the entry of exotic species (Le Houérou 1991; Holmgren et al. 2000), mostly ruderals and weeds (Casado et al. 2015), but also the disassembly of the native herbaceous communities. The capacity of adaptation of these exotic species to the above-described agricultural system (Baker 1974; Figueroa et al. 2004; Castro et al. 2005), the possible exclusion of native species by alien competitors (Callaway and Aschehoug 2000; Callaway and Ridenour 2004), and the existing processes that facilitate the progressive entrance of new exotic species (Simberloff and Von Holle 1999; Madrigal et al. 2011) could determine that the colonizer species reach a competitive advantage over native ones. The result of these processes would be the selection of a small set of native species, generally annual ones, adapted to the new environmental conditions (Arroyo et al. 2000), and showing a lower level of segregated community pattern than colonizers do. Related to this, rapid processes of disassembly of animal communities by invasive species have been highlighted in other studies (Sanders et al. 2003). Additionally, the longer period of co-existence that colonizer species have gone through in Spain, together with their long history of adaptation to the conditions imposed by the silvopastoral system (Arianoutsou et al. 2013), might have favored a more segregated distribution to face the environmental heterogeneity imposed by the new Chilean cultural landscape than Chilean exclusives ones.

Establishment of European agricultural systems in Chile's Mediterranean region has altered the structure of the original herbaceous communities (Turner et al. 1995; Pauchard et al. 2004; Castro et al. 2005). Our results suggest that, under a process of vast colonization as the one contemplated in this study, the species spatial organization patterns cannot be understood when considering all species together. The process of disassembly is shown in our study by the spatial structure of the Chilean native species which have overcome this process, in a less segregated level than the exotic species that became naturalized in Chile.

Naturalización transcontinental de especies herbáceas en pastizales mediterráneos españoles y chilenos

Transcontinental naturalization of herbaceous species in Spanish and Chilean Mediterranean grasslands

Chapter 5 Community ontogeny along a secondary successional gradient

"Real magic in relationships means an absence of judgment of others"

Wayne Dyer

Adapted from: Martín-Forés I, Castro I, del Pozo A, Sánchez-Jardón L, Acosta-Gallo B, de Miguel JM, Ovalle C, Casado MA. Disassembling the myth of invasive species as enemies: the coexistence between aliens and natives along succession in Chilean Mediterranean grasslands. Plos ONE (In review)

INTRODUCTION

The idea of invasive species commonly involves the negative connotation of damage to ecosystems, considering all invasive species as harmful enemies or weeds responsible for declining native biodiversity (Humphries et al. 1991), or causing devastating consequences at ecosystem level (Levine et al. 2003; Vilà et al. 2011). Nevertheless, little is known about the interactions of native and alien plant species forming a new community after a disturbance (McDougall and Turkington 2005), and studies examining long-term effects of alien species in mixed native/alien species communities are scarce (Lodge 1993; Meiners et al. 2002; Suding et al. 2004; Sax and Gaines 2008). Previous studies pointed out that when biological invasion starts, alien species reach areas where they have never been before and interact with native species which they did not previously evolve with (Heger and Trepl 2003; Cox 2004). This implies new biotic interactions (Saul et al. 2013) driving community assembly (Corbin and D'Antonio 2004; Cramer et al. 2008) and ontogeny (Magro et al. 2014) in the invaded area, which could be a determinant for the success or failure of those invasions. This scenario allows potential insight into patterns of life-form replacement in alien and native species groups, possible exclusion of natives as a consequence of the effects of alien invaders as previously observed by Orrock et al. (2008), and relationships, whether negative (competence), neutral (tolerance), or positive (facilitation) between them.

Although the classic idea of ecological succession has been present in ecological literature for several decades (Walker and del Moral 2003), its popularity has decreased and the knowledge provided by it has not been appropriately integrated in biological invasion studies (Catford et al. 2009; Prach and Walker 2011). To understand alien plant behavior it is important to not only to consider the time of introduction and a broader temporal range (Suding et al. 2004; Cramer et al. 2008), but also community assembly with natives along secondary succession (Catford et al. 2009; Prach and Walker 2011). Thus, succession studies can provide the necessary conceptual basis to explore how the dynamics of community assembly operate, as well as to understand the role of alien species in the process of ontogeny of mixed native/alien communities.

Previous studies proposed that dynamics of vegetation communities may be altered due to biological invasions that occur after disturbances (Meiners et al. 2002; Cramer et al. 2008). A number of studies have shown that disturbed sites are more susceptible to being invaded than undisturbed ones (Groves and Burdon 1986; Davis et al. 2000; Young et al. 2001; Shea and Cheasson 2002; Catford et al. 2009; Gurevitch et al. 2011), particularly in post-agricultural lands (Rejmánek 1989; Meiners et al. 2001). After disturbances, novel niche opportunities are created (Johnstone 1986; Shea and Chesson 2002) of which aliens can take advantage. This can be explained by the empty niche hypothesis (Simberloff 1995; Hierro et al. 2005), and the concept of opportunity window (Shea and Chesson 2002; Catford et al. 2009). In this context, Chilean post-agricultural grasslands, currently used for livestock grazing, constitute an excellent scenario for studying patterns of invasion by alien species and community assembly associated with ecological secondary succession, due to the high percentage (49%) of aliens they contain (Martín-Forés et al. 2012). The novelty of the present study relies on the lack of previous reports relating community ontogeny with invasive effects in mixed alien/native herbaceous communities typical of Mediterranean grasslands.

Thus, the main aim of this study is to evaluate the relationship among native and alien species which show an invasive behavior (*sensu* Richardson et al. 2000), by studying patterns in community ontogeny associated with secondary succession. The two types of disturbance considered in this study (grazing and plowing) are considered the main drivers favoring higher diversity and abundance of alien plant species (Jauni et al. 2015), so we hypothesize that a detriment of native species will occur along succession due to the effect of alien species in the community.

MATERIAL AND METHODS

Study area

The study was conducted in four farms (sites) located in the eastern part of the coastal mountain range (34°42'-36°32' S and 70°18'-72°47' W), in the administrative region of Maule, within the Mediterranean region of Central Chile: Culenco (CU), El Álamo (EA), Patagua (PA) and Santa Dolores (SD). The region is dominated by savannah-like grassland known as espinal, formed by scattered trees of *Acacia caven* and a herbaceous matrix of native and exotic species almost exclusively from the Mediterranean Basin (Ovalle et al. 1990). In order to reduce variability, management practices, topography, and substrate were similar in all selected sites. The mean annual temperature in this region is 14.7°C, the mean minimum is 4.7°C (July) and the maximum 27.0°C (January). Long-term average annual precipitation is 695 mm, with a six-month (November—April) dry season. Topography in all studied sites was hilly without pronounced steep slopes and soils were slightly acidic and presented low nutrient content: less than 20 ppm of N, 2-3 ppm of P and 1-2 % of organic matter.

The land use system in all these farms is based on a crop-pasture rotation where paddocks with crops (mainly wheat) coexist with grasslands covering a wide temporal gradient since cultivation abandonment. For crop establishment the soil is ploughed in spring and maintained as fallow till the next autumn when the crop is sown, using conventional tillage and moderate levels of fertilization. After crop harvest, semi-natural grasslands dominated by annual species are established which remain for several years or even decades. These grasslands are used for extensive grazing. During the first years these grasslands are grazed mainly by sheep (stocking rate ranging between 1.5 – 3 sheep/ha), and later by cattle, mostly during winter, in order to avoid running out of pastures in summer period (Fig. 21).

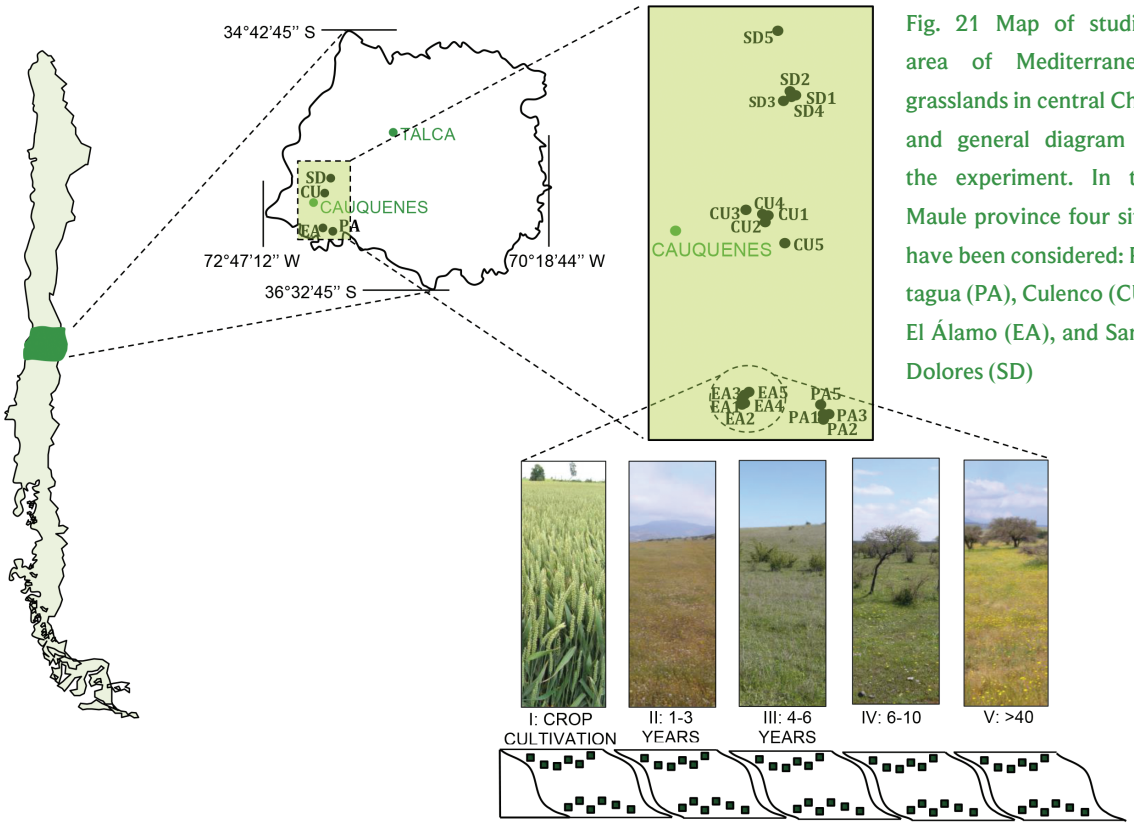

Fig. 21 Map of studied area of Mediterranean grasslands in central Chile and general diagram of the experiment. In the Maule province four sites have been considered: Patagua (PA), Culenco (CU), El Álamo (EA), and Santa Dolores (SD)

Data collection

Vegetation surveys were conducted in paddocks of different age since cultivation at each of the four farms in spring 2011 (late October and early November). The surveys were more concentrated during the first decade of abandonment, since community dynamics is faster during the early successional stages (Peco 1989; Pineda et al. 1981). Therefore, at each site, five ages were considered: crop cultivation including their weed species (stage I), one to three years (stage II), four to six (stage III), six to ten years of abandonment (stage IV), and finally, grassland communities abandoned more than forty years ago (stage V). In the Patagua (PA) site no paddocks with 6-10 years of abandonment existed, therefore only four situations were sampled (stages I, II, III and V). In order to consider the possible influence of water availability between slope positions in plant species composition (Casado et al. 1986; Acosta et al. 2008), vegetation at each site and age stage was evaluated in two 10 x 10 m plots located on the upper and lower zone of a gentle slope, respectively. The distance between slope zones was always comprised between 50 and 100 m. In each of the 38 plots (4 sites x 5 successional stages (except at PA) x 2 geomorphological positions), six 50 x 50 cm quadrats were randomly distributed where total plant cover and the presence of all occurring species was assessed **(Fig. 21)**. Quadrats were always situated in open areas to avoid the influence of *Acacia caven* trees on species composition (de Miguel et al. 2013).

Chilean plant species were classified as native or alien according to Marticorena and Quezada (1985, 1987), and the information provided by the Biological Invasions Lab (LIB) of the Universidad de Concepción (http://www.lib.udec.cl/database.html). Nomenclature of all alien species of European origin were homogenized according to Castroviejo et al. (1986-2014), and in the case of families not reported in this source, according to Tutin et al. (1964-80). For the Chilean native species the nomenclature was standardized according to Zuloaga et al. (2008).

Data analyses

Cultivated species, such as *Triticum* sp. and *Avena sativa* were not considered for the subsequent analyses due to its deliberate human introduction for agricultural purposes. *Juncus bufonius* was also removed from the database because of its native character both in Chile and Spain, therefore, it was difficult to assess whether the individuals found originated in one country or the other. Years since abandonment were log-transformed. An exploratory Detrended Correspondence Analysis (DCA) was carried out to explore the main floristic trends among plots and to know which species were the most determinant in relation to the obtained axes. The influence of slope zone and successional (years since abandonment) gradient on species richness (*i.e.* number of species), was evaluated using different mixed model effects analyses with a Poisson error distribution. Models were fitted considering as response variables total species richness and richness of each species group: native and alien species to Chile; annuals and perennials. We computed all the possible models with log-transformed time since abandonment (TLOG) and slope zone (ZONE) as the explanatory variables (fixed factors), and SITE as the random factor.

All possible models including differing in the structure of fixed effects were adjusted by the Laplace approximation, and the Akaike Information Criterion corrected for small sample size (*AICc*) (Burnham and Anderson 2002) was calculated. The best-fit models (lowest *AICc* and with differences in their *AICc* lower than 2, $\Delta AICc<2$) were selected; in cases where more than one best-fit model resulted, parsimony criterion was applied and the model with a lower number of parameters was chosen for subsequent analyzes. Model validation

of the best-fit model was based on checking the lack of patterns in Pearson and deviance residuals against explanatory variables to assess whether excess variation was due to a misspecified model or not. We also assessed the lack of overdispersion by verifying that the ratio between the sum of squared Pearson residuals and the difference between the number of observations and the number of regression parameters was about 1 (Zuur et al. 2009).

Finally, Spearman rank-sum correlation between native and alien species richness, and Pearson correlations between each of them and total herbaceous cover were also calculated to explain how community assembly evolves along time. These correlations were done at the quadrat scale. Analyses were performed in PCORD (Multivariate Analysis of Ecological Data. Version 6. MjM Software, Gleneden Beach, Oregon, U.S.A) and R (R Core Team 2013) using packages lme4 (Bates et al. 2014) and *AICc*modavg (Mazerolle 2013).

RESULTS

Axis I of the DCA analysis showed a floristic trend associated with time since abandonment (Fig. 22) and explained 25.2% of the variability. Four different groups of herbaceous communities were clearly identified, coinciding with stages I (crop cultivation), II (early succession), III and IV together (mid succession), and V (late succession), respectively. Axis II (16.9% of variability) of the DCA showed some floristic differences among sites, possibly associated with their own stories of land use or local variations, which are outside the scope of this study. Given this variation independent of time, sites have been further considered as random effect in mixed models.

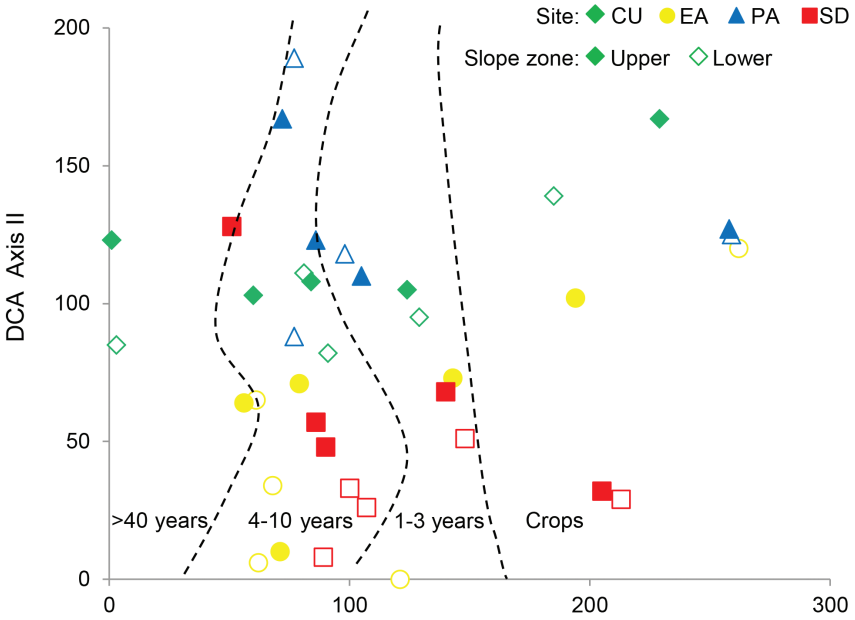

Fig. 22 Scatterplot showing the distribution of sampled herbaceous communities in the two first axes obtained in the DCA analysis. Different symbols correspond to sampled sites: triangles (Patagua, PA), squares (Culenco; CU), circles (El Álamo; EA), and diamonds (Santa Dolores; SD). Open symbols represent lower zones of the slope, while close ones represent upper zones

The most representative species of the first stages, crops and post-cultivation, were *Anagallis arvensis, Convolvulus arvensis, Lolium rigidum* and *Plantago lanceolata* (all of them aliens), whereas the most representative species of late successional stage were *Avena barbata, Bromus hordeaceus, Centaurium cachanlauen, Cicendia quadrangularis, Hypochaeris glabra, Leontodon taraxacoides, Piptochaetum montevidense, Plantago firma, Tristeum spicatum and Vulpia muralis* (half natives, half aliens).

According to the geographical origin and life-form, both annual and perennial native species clearly increased with time since abandonment (Table 10). Among annual species, seven were present in every successional stage and 16 (55%) were only present in the two latest successional stages. Among perennial species, ten (37%) were found only of the late-successional stage, and 16 (59%) in the two more mature stages. In the case of alien species, the number of annuals increased slightly in the mid successional stages, doubling the number of native ones (Table 10). Only five perennial alien species were found and these did not show a trend to increase with time since abandonment.

Table 10. Number of species classified by life-form within native and alien species along the chronosequence studied: crop cultivation (SI), one to three years (SII), four to six (SIII), six to ten years (SIV), and more than forty years since cultivation (SV).

	SI	SII	SIII - IV	SV	Total sampled
Natives					
Annuals	9	12	19	25	29
Perennials	3	7	13	21	27
Total per stage	12	19	32	46	56
Aliens					
Annuals	29	42	42	36	60
Perennials	4	1	4	1	5
Total per stage	33	43	46	37	65

The best model for each species group considered, except for number of aliens, was the one that included only TLOG as fixed effect (Table 11). Best models always had highly significant and positive influence of TLOG (*p-value* < 0.001) on species richness, and were significantly different from the null model. In the case of alien richness, the best-fit model was the null model, which only included the random effect SITE. ZONE was not a good predictor in any model, therefore herein both slope zones were considered as replicates.

Table 11. Best fit-models for species richness (response variable) classified as natives or aliens and annuals or perennials. TLOG corresponds to years (log-transformed) since crop abandonment. Models are adjusted by the Laplace approximation.

Response variable	Best model	*AICc*	Correlation of fixed effect TLOG	TLOG coefficient	*p-value* for fixed effect	Variance explained
Total richness	Richness ~ TLOG + (1|SITE)	50.34	-0.883	0.3895	<0.001	40.2%
Native richness	Natives ~ TLOG + (1|SITE)	44.72	-0.807	0.9643	<0.001	69.1%
Aliens richness	Aliens ~ 1 + (1|SITE)	43.89	-	-	-	-
Number of annuals	Annuals ~ TLOG + (1|SITE)	53.65	-0.880	0.2944	<0.001	24.2%
Number of perennials	Perennials ~ TLOG + (1|SITE)	43.08	-0.867	1.0697	<0.001	57.4%

According to the selected models, positive relationships were obtained between time since abandonment and total and native richness ($r = 0.55$, and $r = 0.79$, respectively), whereas no significant relationships were found for alien species richness (Fig. 23).

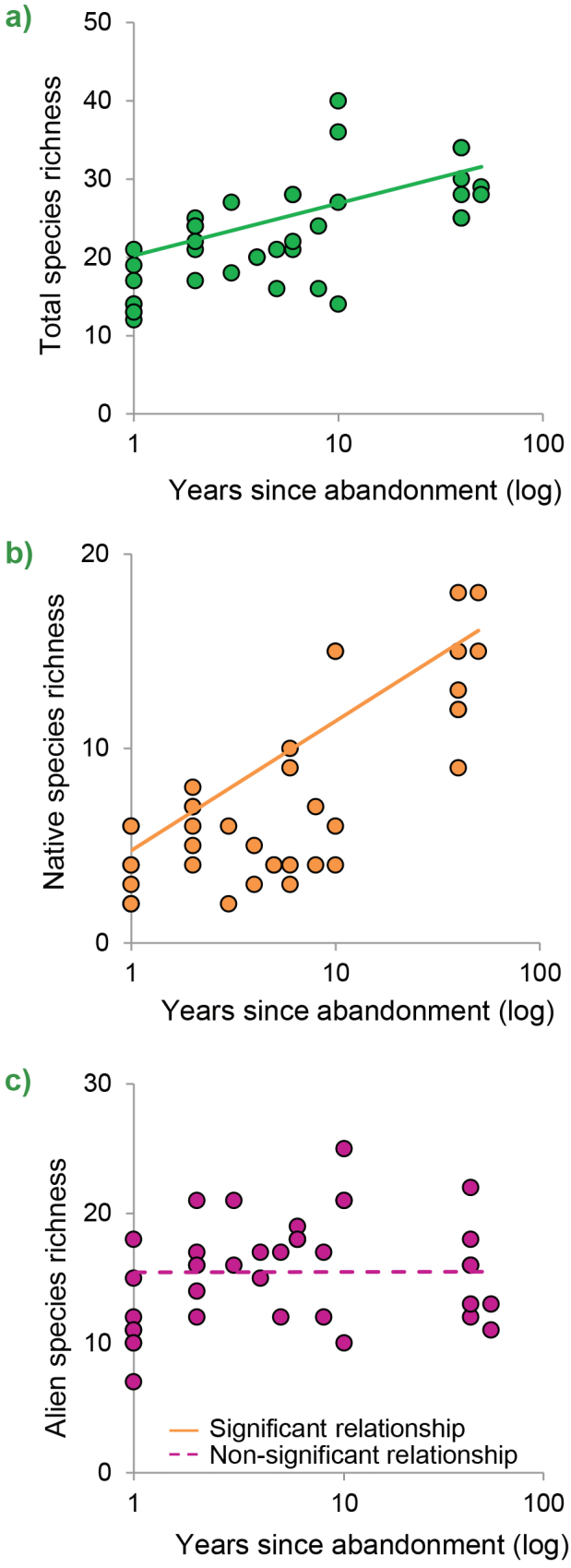

Fig. 23 Relationship between years since abandonment (log-scale) and (a) total, (b) native, and (c) alien species richness recorded in all sites. Adjustments between pairs of variables are shown, whether relationships are significant ($p \leq 0.05$) or not

Total herbaceous cover increased with time since cultivation (positive correlation, $r = 0.233$, $p < 0.0001$). Considering the quadrat unit, correlation between native and alien species richness was negative and significant during the crop stage and the first three years since cultivation, became positive after that, and not significant in communities with more than 40 years old (Fig. 24a). Relationships between species richness and total herbaceous cover had different behavior for native and alien species depending on the time since cultivation (Fig. 24b). During the crop stage this relationship was significant in both groups of species but positive for natives and negative for aliens. After one to three years since cultivation abandonment only native species showed a negative correlation. At intermediate and mature stages of succession species richness of both species groups had the same tendency: negative for four-ten years old communities and not significant for more than 40 years old communities.

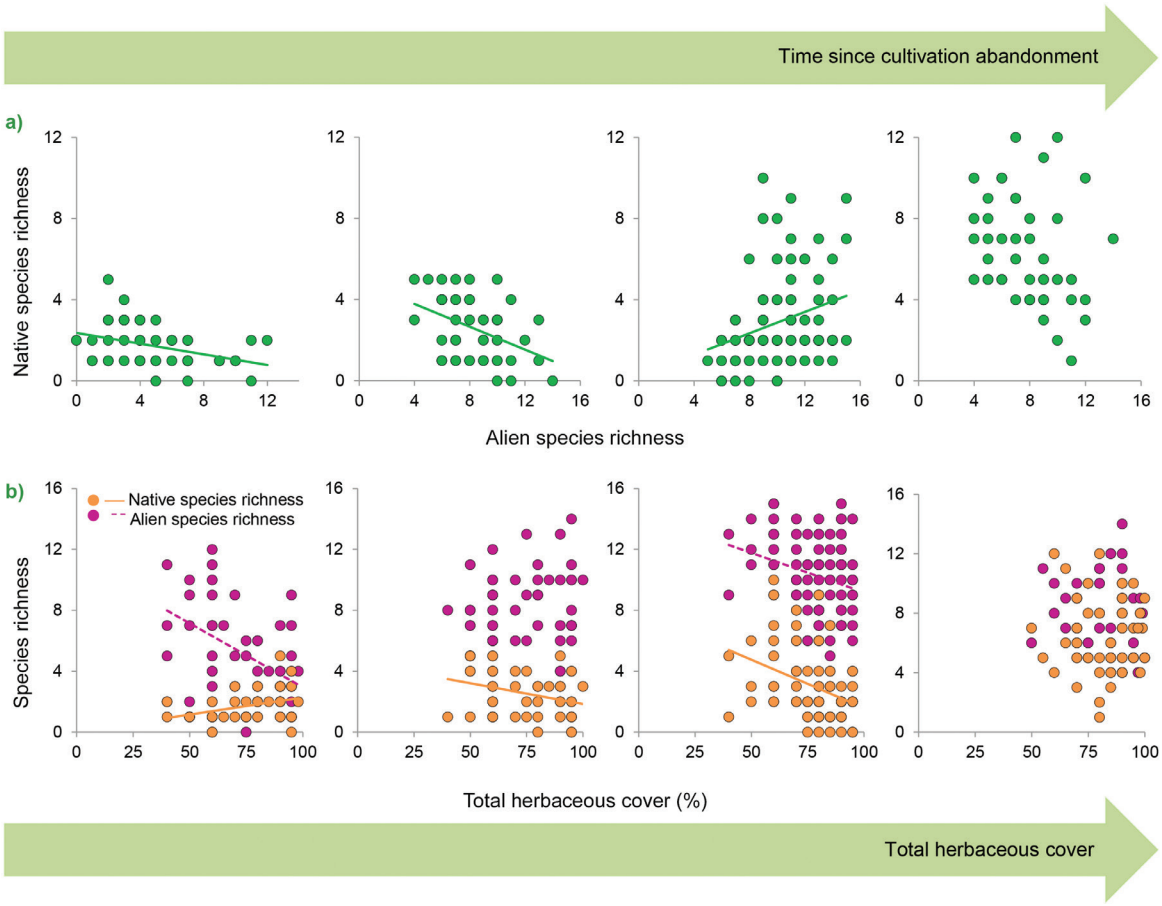

Fig. 24 Correlations between a) native and alien species richness and between b) herbaceous cover and native and alien species richness. Only significant relationships ($p < 0.05$) are shown with lines. Graphs are sorted following the studied chronosequence: crop cultivation (S1), one to three years (S2), four to ten years (S3), and more than forty years since cultivation (S4)

DISCUSSION

Patterns of species and life-form along secondary succession

Grazing and anthropogenic disturbances are considered the main factor promoting higher diversity and abundance of alien plant species (Jauni et al. 2015). In our study design both types of disturbance are included: we analyzed vegetation recovery after an intense disturbance event (*e.g.* plowing and crop harvest) wherein the successional process overlaps with a low intensity but continuous disturbance by grazing. Within this framework, and in accordance with classical successional studies, the structure of grassland communities of central Chile changes through time, with rapid replacements in species composition at the first stages that become slower in later stages (Pineda et al. 1981). The gradual substitution of species with time can result in a clear differentiation of plant communities as the successional process advances.

Most studies of long-term succession considering exotic and native species detect a decrease of alien species richness along time (Meiners et al. 2002; Tognetti et al. 2010). They also highlight a fall in annual species (or at least herbaceous ones), that are replaced by woody species (Meiners et al. 2002; Tognetti et al. 2010; McLane et al. 2012). However, our results constitute a novelty regarding how richness of native and alien species and life-form replacement patterns change along succession. Time since cultivation abandonment has a positive effect on native species richness, whereas alien species increase after the first year of abandonment and remain stable until the end of the chronosequence. In the same way, life-form replacement patterns appear to be closely associated to the origin of species; both annual and perennial species increase with succession, being perennials almost exclusively represented by natives. These successional trends determine as final result a community dominated by herbaceous species where species of different geographic origins and life-forms coexist. In this ecosystem woody plants colonization ability is almost null due to the pressure exerted by grazing. This factor determines the maintenance of a herbaceous grassland structure and prevents the development of a closed canopy of woody plants, responsible for the decline of herbaceous and exotic species detected in other studies (Meiners et al. 2002; McLane et al. 2012).

Drivers for structuring plant communities through time

Compared to the above descriptive approach of successional patterns, our results allow analyzing the mechanisms responsible for these temporal changes. However, it should be noted that our results are based on observational data on which the positive or negative interactions between species have not been evaluated directly. Further experimental research on these plant-plant interactions would be desirable to validate some of the interpretations drawn here.

The process of community re-establishment (or community ontogeny *sensu* Magro et al. 2014) can be interpreted in the context of successive biotic and abiotic drivers acting in a different way through time (Armas and Pugnaire, 2005; Armas et al. 2013; Jeffers et al. 2015). Many studies have indicated a similar role of native and exotic species along secondary succession (Meiners 2007; Tognetti et al. 2010; McLane et al. 2012). However, our results indicate that, at least during the early successional stages, the behavior of the species is very dependent on their geographical origin (Table 10).

The plowing causes a drastic disturbance that drives colonization responses according to species' strategy. Our results show a negative correlation between alien and native species at local scale in earlier stages of

succession (Fig 24). The existence of negative correlations between native and exotic species richness has been considered an indicator of competition (Cleland et al. 2004; Bartomeus et al. 2012). However, the fact that alien richness exhibits a decline with herbaceous cover whereas native richness increases with it, suggests a segregation of niches between both species groups more than an effective competition. In these early successional stages the empty niches created by cultivation abandonment are preferentially occupied by alien species (negative correlation between alien species richness and total herbaceous cover; Fig 24b). The increase in cover associated with this colonization appears to create the appropriate conditions for the arrival of native species (positive correlation between native species richness and total herbaceous cover; Fig 24b). The native Chilean Mediterranean flora rarely includes adaptations to high intensity disturbances typical in the Mediterranean basin, like fire, tillage or long-term grazing regime. In fact, fire events were absent in the Chilean Mediterranean region before the Spanish conquest (Aronson et al. 1998; Figueroa et al. 2004) except for some aboriginal fires at a small scale (Veblen and Lorenz, 1988). Long-term grazing regimes by herbivores was also absent (Jaksic 1998) until the European's arrival, although there were some camelids (guanaco, llama and alpaca) with probably low grazing impact (Aschmann 1991). The drastic landscape anthropic transformation in the last centuries due to agricultural practices not only reduced native flora but could also create opportunity windows (Tilman 1997; Zobel et al. 2000) for alien invaders. These species take advantage of post-agricultural grasslands, successfully colonizing empty niches at the beginning of community ontogeny (which agrees with Cramer et al. 2008; Baer et al. 2009; Tognetti and Chaneton, 2012; Jauni et al. 2015). The idea of eco-evolutionary experience proposed by Saul et al. (2013) states that alien invaders have been adapted to disturbances caused by agricultural practices in their area of origin for several centuries (Prinzing et al. 2002), while Chilean native species might not be pre-adapted to changes in their environmental conditions (Sher and Hyatt 1999). The species that arrived to the Mediterranean-climate region of Chile belong mainly to two types of donor plant communities: ruderals (those associated with anthropic disturbed sites which generally comprise nutrient-demanding annual species), and annual crop weeds associated to arable lands (Casado et al. 2015). Both alien ruderal and weeds species are the most representative plants found in early-successional communities, proficient in colonizing novel niches provided after an anthropic disturbance (Catford et al. 2009). After this first colonization phase, and as the herbaceous cover increases, there is a change in species composition as well as a readjustment of the role of native and alien species. Correlation between both species groups becomes positive, which agrees with Compagnoni and Halpern (2009), indicating that similar factors are determining the diversity of both types of species (Levine and D'Antonio 1999). Native species increase in number despite the fact that previous studies suggested that alien species are generally competitively superior (D'Antonio and Mahall 1991; Fogarty and Facelli 1999), or are able to aggressively displace previously established species (Young et al. 2001). This result suggests that alien invaders do not inhibit the establishment of native species, which is in accordance to the idea that competition is not important in transcontinental naturalization of alien species in Chile (Martín-Forés et al. 2015) and to the ''passenger'' model proposed by Macdougall and Turkington (2005). Continued grazing is one of the factors that may be attenuating interspecific competition (Graff et al. 2007; Jauni et al. 2015), favoring an increase in the number of native species, as has already been highlighted in the Mediterranean grasslands of Chile (del Pozo et al. 2006).

Finally, when considering mature grasslands (more than 40 years since cultivation abandonment) the relationship between native and invasive alien species becomes non-significant, indicating that native and alien plants are assembled together comprising an entire balanced community.

As a consequence of the high percentage of aliens together with the rich Chilean native flora observed in mature grasslands of the studied area, two important questions arise: would invasive species spread or even transform the conditions of the ecosystem without causing biodiversity loss? Could they even constitute an advantage for native plant species? In this sense, although the importance of alien species decreases slightly and natives predominate within this herbaceous community, it seems to be a 'pacific coexistence' between both groups of species. This coexistence may be favored by the different response of native and alien species to the continued grazing. Most of the alien species base their persistence in high reproductive capacity against livestock consumption (*e.g. A. barbata, B. hordeaceous, L. taraxacoides or V. muralis*; see Table 4 in de Miguel et al. 2010). By contrast, native species have small size (*e.g. C. quadrangularis, P. firma*) or low palatably (*e.g. P. montevidensis, C. cachanlauen*), traits that are associated to a defensive strategy to grazing (de Miguel et al. 2010).

In summary, contrary to recent studies (Kulmatiski 2006; Vilà et al. 2011; Tognetti and Chaneton 2012) stating that alien species which got established in early successional stages impeded the re-establishment of native ones, our results show no apparent competition between alien invaders and Chilean native species along community ontogeny associated to secondary succession. During this ontogenic process, alien and native species seem to play a complementary role. In a first phase, ruderal and weedy crop alien species are capable of successfully established under the disturbed post-agricultural conditions for which native species are not adapted. In a second phase the community is made up of native and exotic species, although such coexistence is based on two differentiated strategies: grazing-tolerant species (mainly alien species) or grazing-defensive species (mainly native species). Consequently, community ontogeny along succession seems to constitute a net gain of natives after disturbance, compatible with the maintenance of a general alien pool, allowing the 'pacific coexistence' of both of them, therefore disassembling the myth of the damage caused by the invasive enemy. Further research would be desirable to specifically assess whether aliens may facilitate the establishment of natives by modifying and ameliorating these harsh physical conditions after disturbances or not.

Naturalización transcontinental de especies herbáceas en pastizales mediterráneos españoles y chilenos

Transcontinental naturalization of herbaceous species in Spanish and Chilean Mediterranean grasslands

Chapter 6 Mechanisms of adaptation

"Enjoying success requires the ability to adapt. Only by being open to change will you have a true opportunity to get the most from your talent"

Nolan Ryan

Martín-Forés I, del Pozo A, Acosta-Gallo B, Avilés M, de Miguel JM, Ovalle C, Sánchez-Jardón L, Castro I, Casado MA. Phenotypic comparison of three Mediterranean herbaceous species in common gardens in Spain and Chile reveals great plasticity and ecotypic adaptation. Biological Invasions (in review)

INTRODUCTION

A large number of plant species from the Mediterranean Basin were accidentally introduced in Chile and became naturalized in the Mediterranean region (Martín-Forés et al. 2012) associated with the Spanish conquest and the human breakdown of biogeographic barriers to dispersal (D'Antonio and Vitousek 1992). Some of these species are currently distributed over a wide range of the Chilean Mediterranean climate region. These exotic species encounter new abiotic and biotic conditions including drought period, habitat characteristics, latitude, photoperiod, land use patterns, livestock grazing, and community interactions (such as facilitation and competition processes). Despite the short history of these introduced species in Chile (probably no more than 450 years), they might have faced a process of genetic and phenotypic differentiation, which allowed them to adapt to the new conditions (Maron et al. 2004, 2007) and consequently developed new ecotypes, different from those in Spain.

It is known that ecotypic variations may occur very quickly in annual Mediterranean species (Cocks et al. 1982; Small and Lefkovich 1986; del Pozo et al 2000), when diasporas have been transported beyond the initial distribution center. For example, ecotypic differentiation has been observed in leguminous species related to climatic factors, such as days to flowering and seed hardness in various annual species in Syria (Ehrman and Cocks 1990, 1996), days to flowering in subterranean clover collected in Sardinia (Piano et al. 1996), days to flowering and winter growth of *Medicago polymorpha* in Chile (del Pozo et al. 2000, 2002a, b), or aerial growth of *M. polymorpha* in Sardinia (Loi et al. 1993). Also, in non-leguminous annual species ecotypic adaptations to environmental gradients have been described (Fox 1989; 1990; Neuffer 1990; Galen et al. 1991; Aronson et al. 1992; 1993).

Phenotypic plasticity is another mechanism by which plant species can cope with environmental variability (Baker 1965; Valladares et al. 2005; Rejmánek et al. 2005; Richards et al. 2006; Pyšek and Richardson 2007). For instance, in the invasive Asteraceae, *Taraxacum officinale*, both plasticity and ecotypic adaptation for various traits have been found in relation to latitudinal (Molina-Montenegro and Naya 2012) or altitudinal (Molina-Montenegro et al. 2012) distribution. Plasticity is not always adaptive or improves plant performance (Molina-Montenegro et al. 2010), and could occur simultaneously with ecotypic differentiation (Molina-Montenegro et al. 2013). According to McDowell (2002) and Funk (2008) plasticity of invasive species is higher than that of non-invasive and co-occurring native ones. However, further knowledge about the role that plasticity plays (Chambel et al. 2005), especially in plant species with an invasive ability is still scarce.

Among the 548 exotic herbaceous species described in central Chile, the best represented families at country scale are Poaceae (20% of species), Asteraceae (14%) and Fabaceae (10%) (Martín-Forés et al. 2012). Two representatives of the Asteraceae family, *Leontodon taraxacoides* (Vill.) Mérat. subsp. *longirostris* Finch and P.D. Sell (synonym: *Leontodon saxatilis* Lam. subsp. *rothii* Maire) and *Hypochaeris glabra L.*, and one Fabaceae, *Trifolium glomeratum L.*, are widely distributed in both Spain (the source area) and Chile (the recipient area) (Casado et al. 2015). In this study we evaluate differences in adaptive traits (*i.e.* plant survival and development, biomass and seed production) of the three species collected from different populations of Spain and Chile and cultivated in common garden (CG) conditions in both countries.

The main aim of this study is to detect which adaptive mechanism —plasticity or ecotypic adaptation— predominates in the colonization process of the three selected species. On the one hand, whether the development of a given population varies under different environmental conditions *(i.e.* between CG emplacement), phenotypic plasticity will be occurring; specifically, we hypothesize that the species development will be faster

in the CG with longer drought period and day length. One the other hand, whether plant development under the same environmental conditions (*i.e.* each CG) varies among different populations, ecotypic adaptation will be occurring; specifically, we predict i) that related to longer residence time of the species, Spanish populations will show higher ecotypic differentiation than Chilean ones, and ii) that related to differences in environmental conditions among collection sites, a delay in plant development will occur in those populations coming from places with higher annual precipitation.

MATERIAL AND METHODS

Study area

The study was conducted in the Mediterranean regions of Central Chile and Spain. In Chile, samples were collected in the *espinal* ecosystem, across an extensive area between 32°31' to 37°00' S and 70°46' to 72°34' W (~600 km long from North to South), with mean annual precipitation ranging between 300-1200 mm. In Spain, the study was conducted in the *dehesa* ecosystem located in the center-west of the Iberian Peninsula (Extremadura, N Andalusia and W Castilla-La Mancha), from 37°51' to 40°14' N and from 4°23' to 7°02' W, and with mean annual precipitation ranging between 400-1100 mm (Fig. 25). Soils in both regions are slightly acidic, derived from igneous or metamorphic rocks and the topography is hilly. In both countries, the land has been used for extensive livestock grazing, especially sheep and cattle.

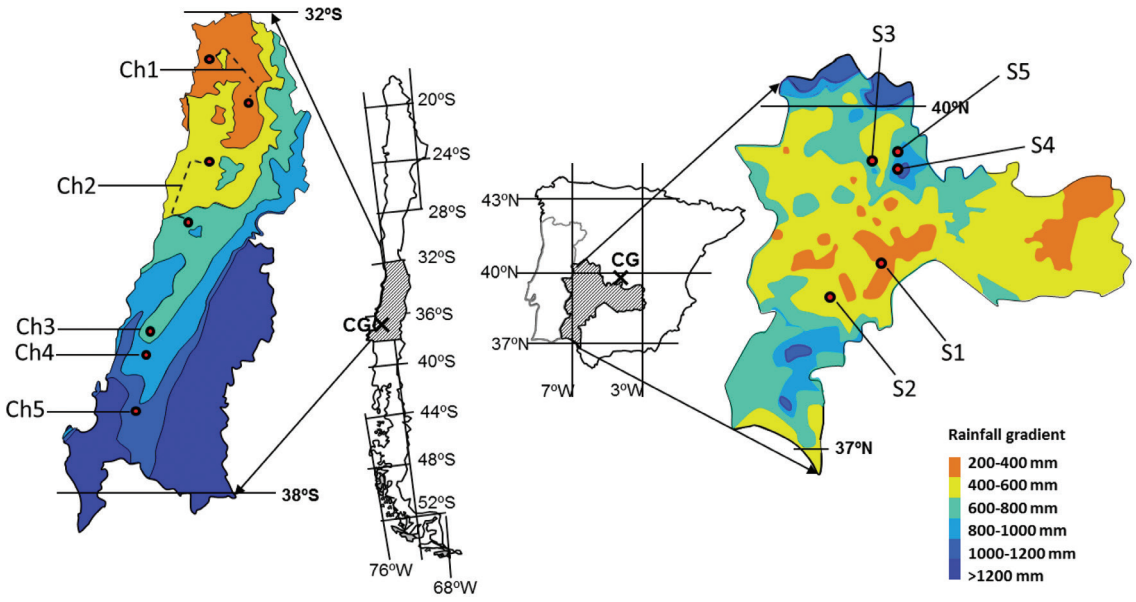

Fig. 25 Map of the studied areas of Mediterranean grasslands in Spain and Chile. Sampling sites of Spain (S) and Chile (Ch) are sorted according to the rainfall gradient. Color tones represent rainfall variability in each country

The *dehesa* contains scattered trees of holm oak (*Quercus ilex* subsp. *ballota*) or cork oak (*Quercus suber*) within a herbaceous layer comprising mainly winter annuals (Joffre et al. 1999; Gea-Izquierdo et al. 2010). It is characterized by very high plant species richness (Pineda and Montalvo 1995). Its vegetation is adapted to a Mediterranean-type climate, characterized by scarce precipitation in summer (drought period from June to September in the Northern hemisphere).

The *espinal* in central Chile's Mediterranean zone is a similar system to the Spanish *dehesa* regarding organization and structure. It presents a savannah-like landscape with scattered trees of espino (*Acacia caven*). Its herbaceous layer is composed by annuals, both native and exotic species, mainly originated in the Mediterranean Basin (Ovalle et al. 1990; Ovalle et al. 2006; del Pozo et al. 2006). The percentage of exotic species it contains is very high (49% according to Martín-Forés et al. (2012)). This high proportion of exotic species in Chile can be explained by its history of land use and disturbance associated with the transformation of the original landscape after the Spanish colonization in the 16th century (Aronson et al. 1998; Arroyo et al. 2000; Figueroa et al. 2004).

Plant material and growing conditions

The three species of study were selected considering the following criteria: they must be 1) species originated in the Mediterranean Basin, 2) typical from grasslands, and 3) abundant enough to present a wide spatial distribution in both countries in order to incorporate climatic variation within them. Those species were *Leontodon taraxacoides, Hypochaeris glabra* and *Trifolium glomeratum*, all of them native to Spain although widely naturalized in Chile. Seeds of these three species were collected in both Mediterranean regions in the spring of 2010, at the end of flowering periods for most plants (*i.e.* May-June in Spain, and October-November in Chile). When existing, we collected mature infructescences from 50 individuals from 15 Spanish populations, and 15 Chilean ones covering a broad rainfall gradient within the Mediterranean region of each country. From the previous 15 populations, a subgroup of five sites was selected in each country. Selected sites were meant to be representative of the whole rainfall gradient and, if possible, the three studied species were contained in each of them. In the driest Chilean sites, *H. glabra* and *T. glomeratum* were not found together in the same site; therefore sites with similar annual precipitation were selected for each species. *L. taraxacoides* was not found in the driest Chilean sites and therefore it was only collected from four Chilean source populations. Geographic coordinates and climate conditions, including annual precipitation, mean annual temperature, and number of months with drought period or water deficit per year, calculated as the number of months in which mean temperature is at least double than precipitation (Bagnouls and Gaussen 1953), were determined at each site (Table 12). For Spain, climate variables were obtained from the State Meteorological Agency (AEMET, http://www.aemet.es) and the Atlas Climático Digital de la Península Ibérica (Ninyerola et al. 2005). In Chile, climate data were obtained from WorldClim (Hijmans et al. 2005), at a resolution of 30 arc-seconds.

Table 12. Geographic and climatic characteristics of the selected populations. TMED is mean annual temperature; PREC is annual precipitation, and MWD the number of months with drought period or water deficit per year.

Country of location	Site	Species collected	Abbreviation	Latitude	Longitude	TMED (ºC)	PREC (mm)	MWD
CHILE	Runge	Tg	Ch1	33°00'25"S	70°53'45"W	14.27	303	8
	Catapilco	Hg	Ch1	32°35'53"S	71°18'50"W	16.19	352	8
	Melipilla	Tg, Hg	Ch2	33°49'18"S	71°18'58"W	17	412	8
	Pumanque	Lt	Ch2	34°37'48"S	71°42'54"W	15.01	719	5
	Boldo	Tg, Hg, Lt	Ch3	35°58'52"S	72°13'38"W	14.33	794	5
	Quirihue	Tg, Hg, Lt	Ch4	36°15'20"S	72°32'58"W	13.14	972	5
	Yumbel	Tg, Hg, Lt	Ch5	37°00'26"S	72°34'01"W	13.33	1168	4
SPAIN	Castuera	Tg, Hg, Lt	S1	38°46'20"N	5°34'48"W	16.89	468	4
	Fuente de Canto	Tg, Hg, Lt	S2	38°16'33"N	6°20'22"W	15.81	572	4
	Madroñera	Tg, Hg, Lt	S3	39°25'23"N	5°47'48"W	15.42	666	4
	Ibor	Tg, Hg, Lt	S4	39°32'53"N	5°22'57"W	14.46	859	4
	Logrosán	Tg, Hg, Lt	S5	39°21'28"N	5°25'04"W	16.17	913	3

Contaminants associated with collected seed capsules were removed in the lab to obtain clean seeds of the three species. Pre-germination experiments employing seeds from 29 populations (three species x five collection sites x 2 countries, except for the driest Chilean location in the case of *L. taraxacoides*) were conducted in Chile (December 2010, and April 2011) and in Spain (September and October 2011). In the case of *L. taraxacoides* and H. glabra, the survival rates obtained were 75% and 100% in each country, respectively. For *T. glomeratum*, the seeds with the highest survival rate were those previously scarified with sulphuric acid 98% for 30 minutes. In the case of *H. glabra* L. and *L. taraxacoides*, species with two morphologically distinct achenes, unbeaked achenes and peripheral achenes without a pappus were respectively selected for being more successful in pre-germination studies (also supported by Imbert 1999, 2002; and Brändel 2007).

Seeds from each collection site were pre-germinated in petri dishes onto filter paper and irrigated with distilled water. They were kept in germination cameras at constant controlled temperature and photoperiod, being 18ºC, and 16/8h light/darkness respectively. From each site of source population and for each species three replicates were always considered for the subsequent CGs. In the Chilean CG, when the plant radicle reached five mm, individuals from each site and replicate were transplanted directly to risebeds at the Experimental Center of Cauquenes-INIA (35°58' S, 72°17' W; 140 m a.s.l.) on the 1st of June of 2012. In the Spanish CG, seedlings were planted in trays filled with a mixture containing 75% of soil and 25% of vermiculite and placed in a germination camera for 11 days. Then, seedlings were transplanted to the field at the Faculty of Agronomy of the Polytechnic University of Madrid (40º26'N, 3º44'W; 600 m a.s.l.) on the 24th of October of 2012. Growing medium containing seedlings of *T. glomeratum* was inoculated with *Rhizobium trifolii* before transplanting into field CG in Chile and Spain.

For each CG emplacement, weekly values of precipitation and daily values of mean temperature were calculated (shown in climatic diagrams in Fig. 26). Those where obtained from a metereological station located nearby the experiments. Source population sites and replicates were randomly assigned to microplots within each CG, getting a total of 87 microplots (3 replicates x 3 species x 5 sites (except the Chilean driest in

L. taraxacoides) x 2 countries). Each microplot occupied an area of 50x100 cm in Cauquenes and 50x200 cm in Madrid. In Chile, ten individuals were planted in each microplot, resulting in a total of 870 plants, whereas in Spain, 20 individuals were considered, 1,740 plants as a whole. Individuals were separated 20 cm between them, whereas the separation between microplots was 30 cm.

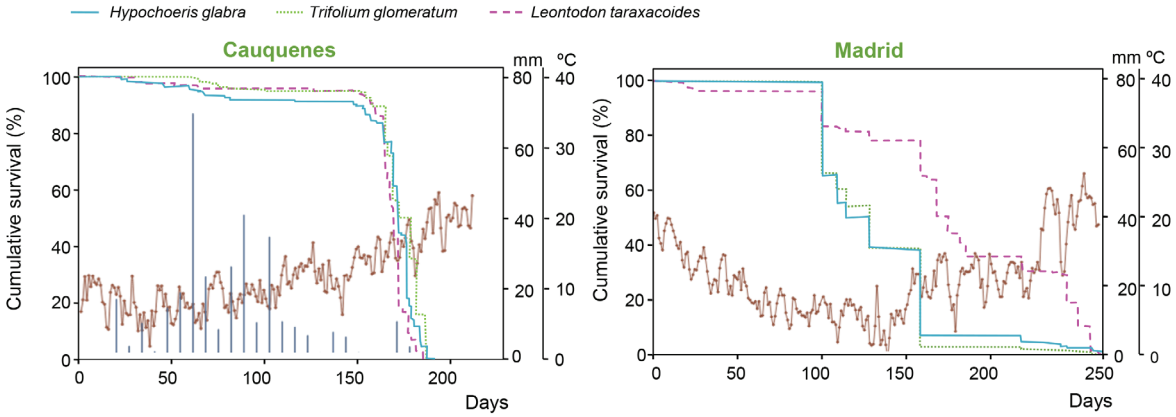

Fig. 26 Kaplan-Meier survival curves of the three studied speciesin both common garden emplacements. Daily medium temperature values (°C) are shown with a continuous red line, while precipitation (mm/week) is represented by blue bars

Data collection

Phenological observations were made three times a week from sowing (S) to flowering and every two days from flowering to plant senescence. The dates when each individual got the first leaf (L), the first floral bud (FL), the first opened flower (FO), the first fruit (FR), and the first mature infructescence (M) were recorded. The date when plant senescence from each species and site was about 50% was also recorded.

Once the individuals reached senescence, plants were harvested. Dried weights of each individual as a measure of above-ground biomass were recorded. Number of inflorescences seed output contained in five infructescences were counted and mean seed output per infructescence was calculated

Data analyses

To check significant differences in survival rates associated with climatic conditions of both CG emplacements, Kaplan-Meier (KM) tests were conducted for the three species in the environmental conditions of each CG.

Also, to evaluate whether phenotypic plasticity or ecotypic differentiation determined significant differences in survival rates, several KM tests were conducted. For each species, KM tests were performed, first for all populations (Chilean and Spanish) in each CG (Cauquenes and Madrid), then separated by population origin (Chile and Spain), and finally for each collection site.

Five phenological phases were calculated: days from sowing to first leaf (S-L), from first leaf to first floral bud (L-FL), from first bud to first opened flower or inflorescence (FL-FO), first opened flower to first infructescence (FO-FR), and from fructification to maturation (FR-M). Bar diagrams with all phenological

phases were then made to assess if phenotypic plasticity and/or ecotypic differentiation were occurring during the plant phenological development.

Regression tests between precipitation in the collection site and days from sowing to 1) flowering, 2) fructification, and 3) maturation were also carried out, as well as between days to flowering and 1) dry biomass weight, 2) number of inflorescences, and 3) medium seed output per infructescence. Regression tests were conducted considering mean values of each replicate and for each country of origin separately, and in case of *L. taraxacoides*, also separately for each CG emplacement. Data analyses were carried out in SPSS 22.0 (IBM 2013).

RESULTS

Climatic conditions of the two Mediterranean regions are different, being rainfall gradient broader and number of months with water deficit higher in Chile than in Spain (Table 12). The cumulative survivals, expressed by the KM curves, of the three species were clearly different at both CGs (Fig. 26). In Madrid CG, *H. glabra* and *T. glomeratum*, and to a lesser extent *L. taraxacoides*, showed an abrupt mortality after 100 days from transplanting, whereas at Cauquenes CG the cumulative survival was 90% until the end of the experiment. The survival of the three species in Madrid was significantly lower than in Cauquenes (Fig. 27). The percentage of individuals of the three species that reached maturation also differed significantly between country of origin and among collection sites (Fig. 27); among populations, significant differences were found in all cases except for *L. taraxacoides* and *H. glabra* from Spanish and Chilean origin, respectively. Trends in the survival percentage at the end of growing season responded to the rainfall gradient for Spanish populations, while among Chilean ones no apparent pattern appeared (Fig. 27). Agreeing with the KM curves showed in Fig. 26, in all the species, the percentage of plants that reached maturity was much lower in Madrid than in Cauquenes CG, no matter the origin of plant populations (Fig. 27).

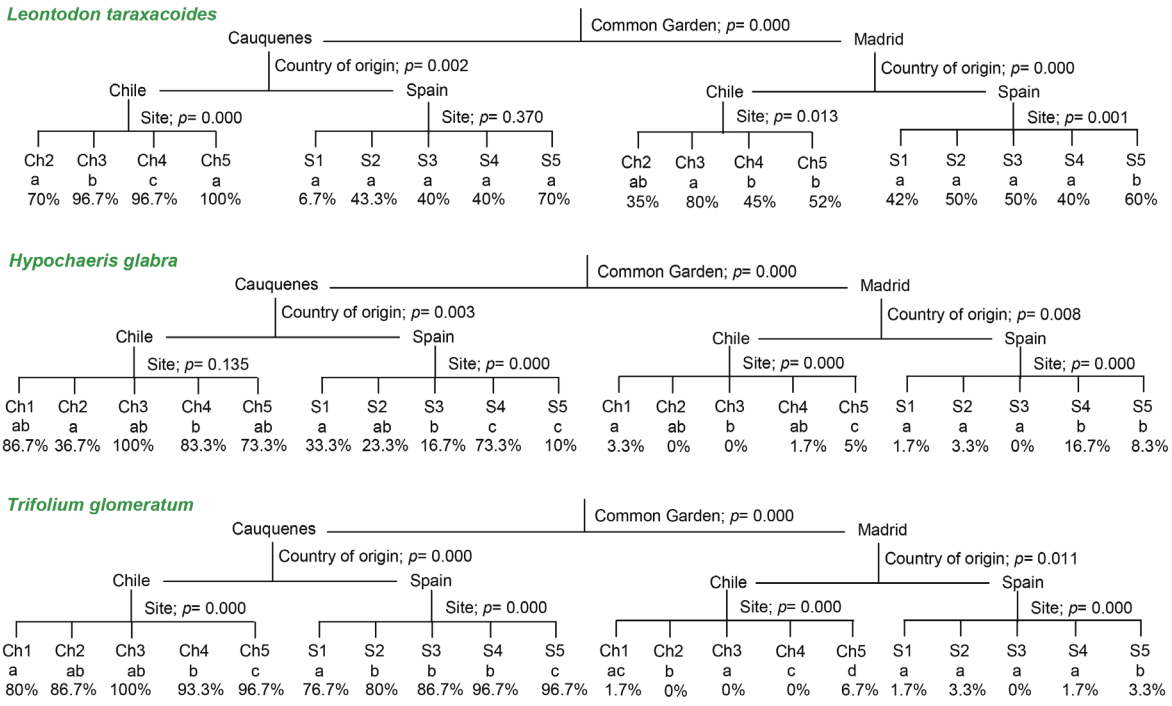

Fig. 27 Tree diagrams for *Leontodon taraxacoides*, *Hypochaeris glabra,* and *Trifolium glomeratum* showing significant differences in survival curves. Each diagram represents the comparison of Kaplan-Meyer curves considering common garden emplacement (first level: Cauquenes vs Madrid), country of origin (second level: Chile vs Spain), and site of the populations (third level: nomenclature as in Table 12). For each site the percentage of survival is shown and the lowercase letters indicate similar groups among sites

Due to the high mortality of *H. glabra* and *T. glomeratum* in Madrid CG, the duration of the different development phases at both CGs was only possible to compare for *L. taraxacoides*. For this species, days to fructification (S-FR) and maturation (S-M) for all populations was much longer in Madrid than in Cauquenes, due principally to the longer duration of the period from sowing to flowering (S-FL) (Fig. 28). Differences in phenology among populations were observed in the three species; in general, populations from wetter environments exhibited longer periods to flowering compared to those from drier environments (Fig. 28). This pattern was particularly evident for *T. glomeratum* from any origin and *H. glabra* from Spain, where differences in days to flowering between the most precocious population (from the driest site) and the latest flowering one (from a humid area) was 27 days. Significant and positive correlations were found between annual precipitation at the collection site and days to flowering, fructification or maturity in populations of *H. glabra* from Spain and of *T. glomeratum* from Chile and Spain (Fig. 29, Table 13).

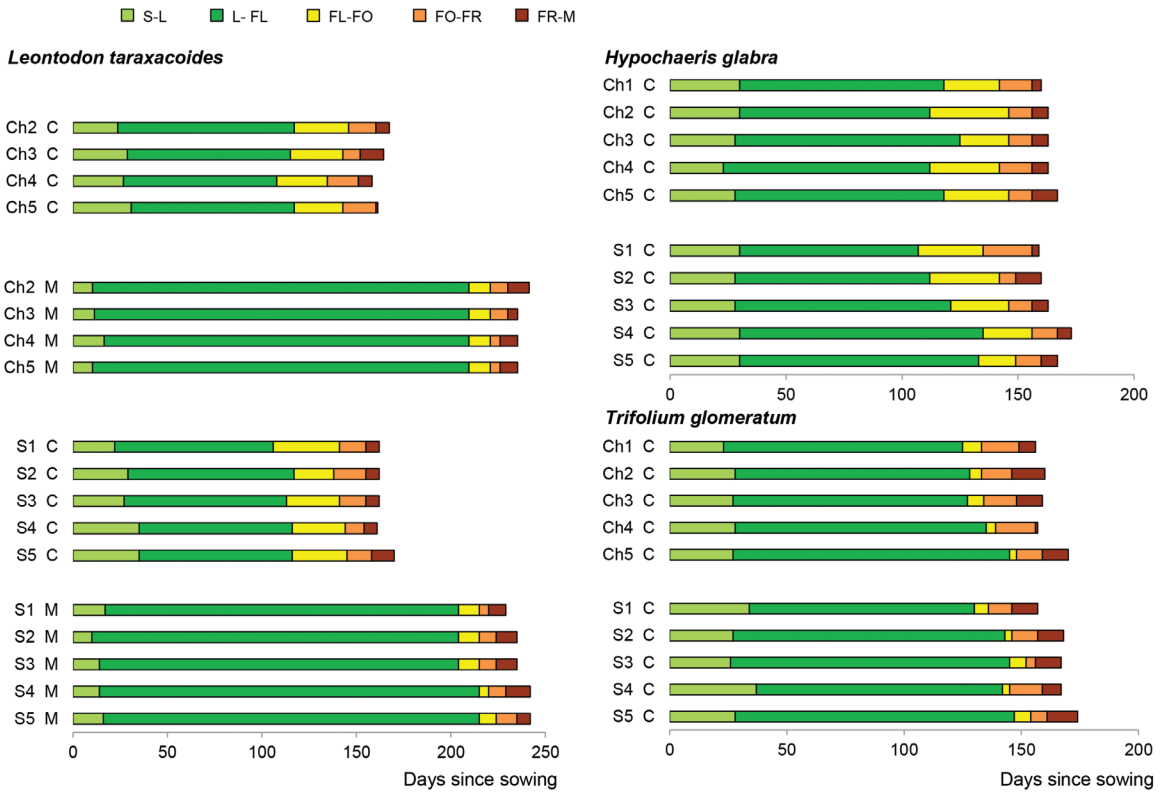

Fig. 28 Phenological development of the three studied species: L. taraxacoides, H. glabra, and T. glomeratum considering days since sowing. Site of seed collection, whether Chilean populations (Ch), or Spanish ones (S) follow a rainfall gradient (from 1, the driest, to 5, the most humid). The common garden emplacement where seed were planted is represented by C (Cauquenes) or M (Madrid). Phenological phases comprise: from sowing to first leaf appearing (S-L), from first leaf to first flower bud (L-FL), form first flower to flower opening (FL-FO), from first opened flower to first fruit (FO-FR), and finally, from first fruit to first mature fruit (FR-M)

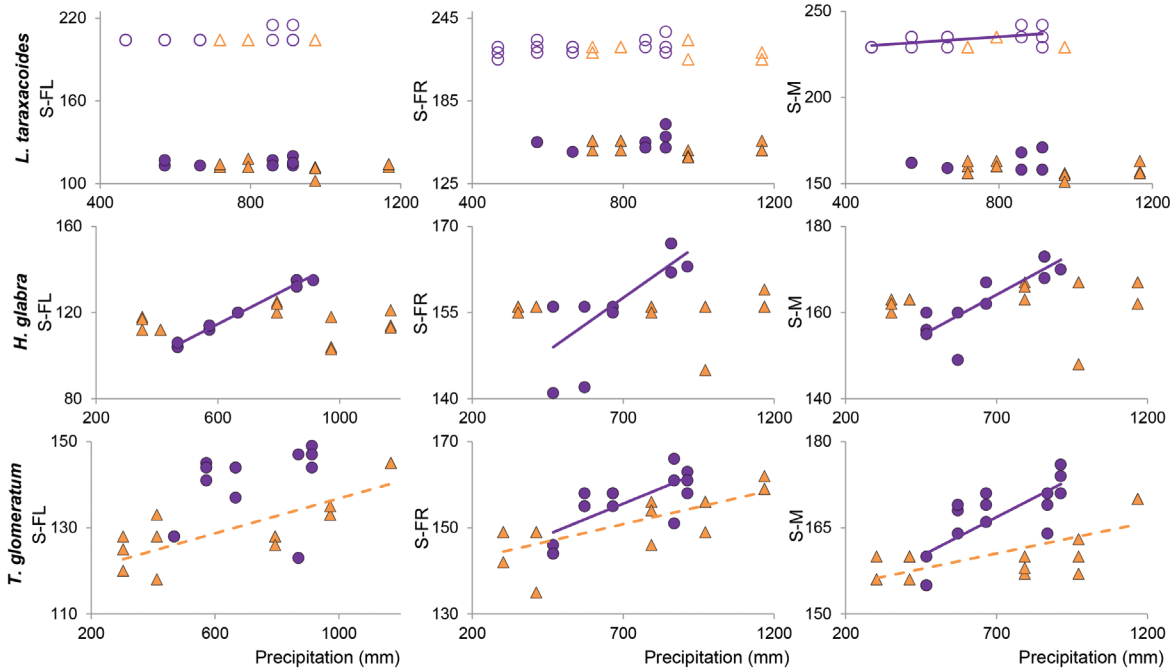

Fig. 29 Relationships between days from sowing to flowering (S-FL), to fructification (S-FR) and to maturation (S-M) and annual precipitation (mm) for the three species. Orange triangles represent Chilean populations, while purple circles represent Spanish ones. Close symbols are used for the common garden established in Cauquenes and open ones for the one in Madrid. Significant relationships are shown by discontinuous (Chilean populations) or continuous (Spanish populations) lines

Table 13. Correlation coefficients and *p-values* (in brackets) for the relationships between precipitation and some phenological phases (S-FL: days to flowering; S-FR: days to fructification; S-M days to maturation) and between days to flowering and some performance indicators. Species populations are differentiated by country of origin (Chile and Spain) and emplacement of the common garden (C: Cauquenes; M: Madrid). Significant values are highlighted in bold.

			Regression between precipitation and			Regression between days from sowing to flowering and		
Origin	**Species**	**CG**	**S-FL**	**S-FR**	**S-M**	**Biomass**	**Inflorescences/ plant**	**Seeds/infructescence**
Chile	*L. taraxacoides*	C	-0. 10 (0.758)	-0.34 (0.273)	-0.30 (0.347)	0.26 (0.413)	-0.21 (0.521)	0.42 (0.178)
		M	-	-0.40 (0.193)	-0.40 (0.201)	-	-	-
	H. glabra	C	0.07 (0.809)	-0.07 (0.814)	0.18 (0.506)	0.01 (0.966)	-0.16 (0.567)	0.40 (0.144)
	T. glomeratum	C	0.81 (0.000)	0.76 (0.001)	0.72 (0.003)	0.58 (0.023)	0.58 (0.024)	-0.246 (0.377)
Spain	*L. taraxacoides*	C	0.22 (0.601)	0.33 (0.420)	0.39 (0.344)	-0.57(0.141)	-0.42 (0.305)	0.02 (0.967)
		M	0.49 (0.075)	0.47 (0.091)	0.58 (0.029)	-0.48 (0.083)	-0.49 (0.076)	-0.68 (0.007)
	H. glabra	C	0.99 (0.000)	0.81 (0.005)	0.87 (0.001)	-0.32 (0.373)	-0.77 (0.009)	0.77 (0.009)
	T. glomeratum	C	0.51 (0.051)	0.75 (0.001)	0.76 (0.001)	0.25 (0.371)	0.19 (0.499)	-0.03 (0.923)

Regarding plant productivity, *L. taraxacoides* did not show any positive significant relationships with days to flowering (Fig. 29). By contrast, in *T. glomeratum*, both plant biomass and number of inflorescences produced per plant were positively correlated with it. In the case of Spanish populations of *H. glabra* the number of capitula per plant decreased and the number of seeds per capitula increased with days to flowering (Fig. 30, Table 13).

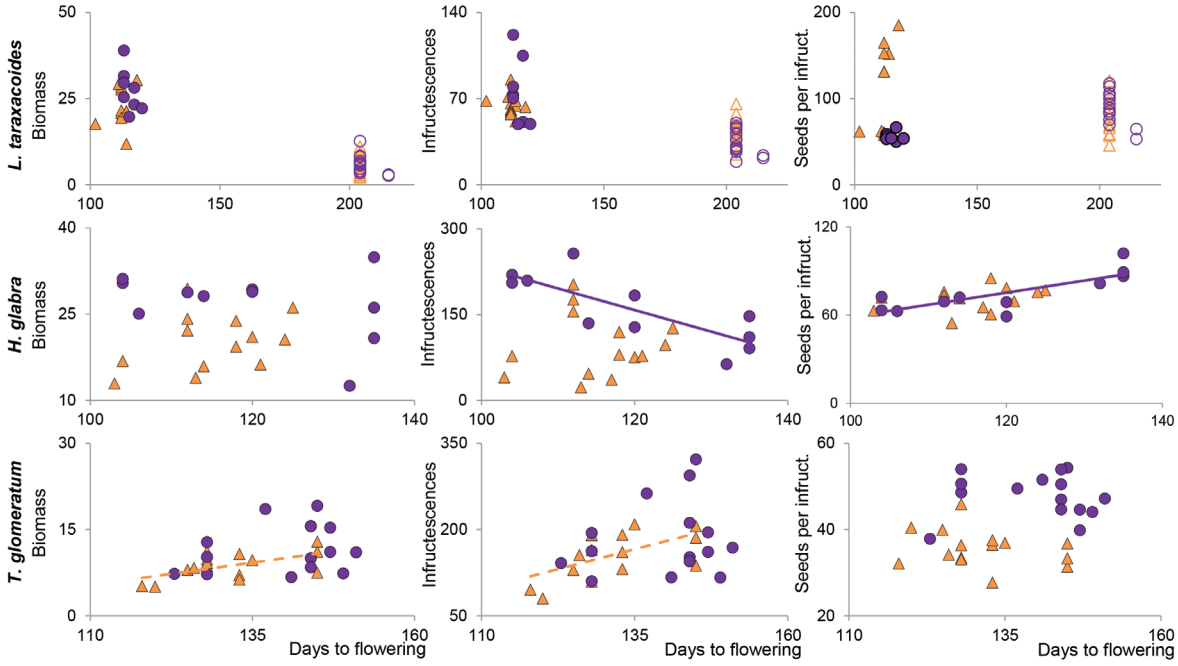

Fig. 30 Relationships between days to flowering (S-FL) and performance indicators –plant biomass, number of infructescences, and medium seed output per infructescence– for the three species. Orange triangles represent seeds from Chilean populations, while purple circles represent seeds from Spanish ones. Close symbols are used for the common garden emplaced in Cauquenes and open symbols for the one in Madrid. Significant relationships are shown by discontinuous (Chilean populations) or continuous (Spanish populations) lines

DISCUSSION

The results obtained show great variability in adaptive mechanisms –plasticity or ecotypic adaptation– for the populations of the three studied species. Nevertheless, the relative importance of each mechanism depends on the species or family considered and/or the variable of analysis: survival rate, phenological development or performance values.

The three species show significant differences in survival rates between the two CGs. Although both CGs have a Mediterranean-type climate, the climatic determinants at regional scale are quite different. In Madrid, temperatures in winter are lower than in Cauquenes, and precipitation is mainly distributed in autumn and spring (Font Tullot 2000), whereas in Cauquenes precipitation occurs mostly in winter months (Aschmann 1973). In addition, during the year of the experiments, the precipitation in Madrid was anomalously scarce (205 days with no rainfall; whereas in Cauquenes there was no rainfall for 125 days) and the temperatures were lower than average (61 days with minimum temperatures below 0°C; only 34 days in Cauquenes) (Fig. 26). These

extreme conditions could explain the high plant mortality observed in Madrid in January, especially in the case of *Trifolium* and *Hypochaeris*. However, differences in survival between both CGs also indicate a high degree of plasticity, especially in *Leontodon*, with capacity to survive even in extreme conditions regardless of the origin of the population. The higher plant survival obtained in populations of Chilean origin and individuals grown in the exotic range, compared to Spanish populations and individuals grown in the native range, respectively, could be related not only to climatic conditions, but also to the 'invasive ability' which seems to appear enhanced in the exotic range of the species (Kumschick et al. 2013).

L. taraxacoides populations growing in both CGs show a delay in time to flowering of more than 70 days in Madrid compared to those growing in Cauquenes. It is known that higher temperatures (Bradley et al. 1999) and longer day length accelerates plant development in temperate species (Molina-Montenegro and Naya 2012). Differences in day length and night length become more extreme at higher latitudes (Bradshaw and Holzapfel 2008), thus, in Madrid the day length or photoperiod is shorter in autumn and winter, but longer in spring and summer than in Cauquenes. These differences in temperature and photoperiod together with the duration of the rainy season makes the drought period lower in Spain than in Chile, allowing the lengthening of the growing season. These results indicate that in *L. taraxacoides* phenological plasticity is greater than the ecotypic differentiation observed among Chilean and Spanish populations.

Ecotypic differentiation seems to be related with the family of the species, as well as with the source population where seed originated. For the Fabaceae *T. glomeratum* our results show significant relationships between precipitation at the collection site and time to flowering, fructification and senescence, no matter the country of origin of plant populations. It also has a positive relationship between days to flowering and biomass, and fruit production but only from Chilean origin populations. This delay in plant development when increased precipitation gives plants more time to invest on biomass production, which confers the ability of yielding more seeds and fruits. Then, it constitutes an indicator of ecotypic adaptation to the environmental conditions where seeds were originated. Similar results were reported by del Pozo et al. (2000, 2002a, b) in another Fabaceae, *Medicago polymorpha*. However, results for Asteraceae were different, showing only ecotypic adaptation in plants of *H. glabra* coming from seeds originated in their native range, but not in those collected in the exotic one (agreeing with Barret and Richardson 1986; Niinemets et al. 2003; and Buswell et al. 2011). Contrarily, populations of *L. taraxacoides* showed greater plasticity and lower ecotypic differentiation (*i. e.* similar times of development independently of the rainfall at the collection sites). Consequently, it seems that different families of plants have different mechanisms of adaption to new environments. Fabaceae, a family with zoochorial dispersion, may need to be more adapted to local conditions of the area of origin and due to its dispersion range, they may have had enough time to develop ecotypic adaptations; Some Asteraceae, such as *H. glabra* and *L. taraxacoides*, have achene dimorphism (Baker and O'Dowd 1982; Brändel 2007), hence not only zoochorial dispersion but also long distance dispersal events by wind —anemochory—, can reach further areas and in this case plasticity could be the most successful mechanism of adaptation.

Additionally, as we expected, seeds from Spanish origin showed more ecotypic differentiation while phenotypic plasticity appeared higher in seeds originated in Chile (in accordance to Alexander et al. 2012). Studied species have evolved in their native range for millennia, while in their introduced range they have only been present for the last centuries, so Spanish populations have had more chances to develop ecotypic and genetic adaptations. On the contrary, although multiple introduction events are common in plants (Dlugosch and Parker 2008) exotic plants established in Chile came from one or a few sites of the Mediterranean Basin, and therefore

with low genetic diversity. Once they arrived to Chile they spread and became adapted to the whole Chilean climatic gradient, at that time they probably had great plasticity to successfully survive to the new conditions.

The fact that species show ecotypic adaptation and/or phenotypic plasticity to face the new environmental conditions could also be related to time since introduction in central Chile. *M. polymorpha* and *T. glomeratum* were first recorded before 1799 and in 1897, respectively (Castro et al. 2005), so they developed in their invaded range for several decades, possibly enough time to develop ecotypic adaptation. In contrast, *L. taraxacoides*, which shows great plasticity, was first recorded in 1963, thus, it has had short time to develop further strategies. Following the same criteria, *H. glabra* from Chilean populations should also have shown ecotypic adaptations because it was first recorded in 1856 (Castro et al. 2005).

Our results suggest that phenotypic plasticity may provide more adaptive skills to successfully adapt to changing environmental conditions (support in results by Geng et al. 2007 and Gratani 2014), as well as to invade new environments. Invasion experience by potential invaders could be associated with increased phenotypic plasticity (related to Dostál et al. 2012); *L. taraxacoides*, the species which most effectively survived in our experiment and therefore showing great plasticity, is the most frequent exotic species in central Chile (Martín-Forés et al. 2012), and is widely distributed due to its invasive character (Martín-Forés et al. 2015) *sensu* Richardson (2000). Such a great plasticity increments the potential of this species to spread in a global changing scenario. Hence, future research including both, ecotypic differentiation but mainly phenotypic plasticity (assessing the species traits that may confer them plasticity and therefore the ability to easily invade new ecosystems) would be desirable especially in relation to global change (Guerin et al. 2014) and conservation strategies.

Naturalización transcontinental de especies herbáceas en pastizales mediterráneos españoles y chilenos

Transcontinental naturalization of herbaceous species in Spanish and Chilean Mediterranean grasslands

Chapter 7 Invasive ability

"He who would learn to fly one day must first learn to stand and walk and run and climb and dance; one cannot fly into flying"

Friedrich Nietzsche

"I always wonder why birds stay in the same place when they can fly anywhere on the Earth. Then I ask myself the same question"

Harun Yahya

Martín-Forés I, Avilés M, Acosta-Gallo B, del Pozo A, de Miguel JM, Sánchez-Jardón L, Castro I, Ovalle C & Casado MA. Plant species colonization, a strategy game: *L. taraxacoides* combines phenotypic plasticity and ecotypic adaptation to enhance spreading in its exotic range.

INTRODUCTION

Colonization of new areas by exotic plants has incremented due to the human overcoming of geographic barriers to species dispersal (D'Antonio and Vitousek 1992), constituting a mayor concern in the current global change scenario (Guerin et al. 2014).

Colonization ability of those alien plants depends on the habitat characteristics of the recipient area (*e.g.* the fluctuating resource availability theory; Davis et al. 2000), as well as on specific traits of the species considered (Pyšek et al. 2009). The first aspect has received considerable attention in the scientific literature (Hejda et al. 2009; Jansen et al. 2011; Kalusová et al. 2013) highlighting that the habitats more prone to be invaded are those more productive or altered (Chytrý et al. 2008; Jansen et al. 2011) normally related with human-made habitats, such as ruderal vegetation and arable land (Lambdon et al. 2008). However, the role played by species traits in the invasion process is still poorly known, due to the lack of relevant information for many invasive plant species (Richardson and Pyšek 2006), and especially to the absence of studies that compare species' traits in their native and invaded territories (van Kleunen et al. 2010a). Nevertheless, some plant traits such as a high rate of growth, a production of numerous small-sized seeds, and plant mechanisms to disperse are tightly correlated with species' invasiveness (Noble 1989; Thompson et al. 1995; Pyšek and Richardson 2007; van Kleunen et al. 2010b).

Plants to successfully arrive, survive, establish, persist and spread in the new environments relay mainly in two strategies, enhancing seed output per plant and achieving long-distance dispersal of seeds (Keddy and Weiher 1999; Rejmánek et al. 2013). Seed output per plant depends on total biomass and the fraction allocated to reproduction (Abrahamson and Gadgil 1973; Amir and Cohen 1990); thus, vegetative and/or reproductive effort can be enhanced in individuals with higher biomass. For its part, effective dispersal increases the probability of a propagule arriving to a new environment to colonize. Seed dispersal mechanisms are inherent of each species and depend on its functional traits (Mossman 2009), thus, the dispersal syndrome of a plant can be inferred from the morphology of its diaspores (Tiffney 1984). In this sense, seed and fruit polymorphism are mechanisms used by plants to face different microhabitats and environmental conditions (Imbert et al. 1996; Imbert 2002), allowing the colonization of highly unpredictable habitats (Harper 1977; Cohen and Levin 1991).

Asteraceae is one of the plant families best represented worldwide by the large number of invasive alien species it contains (Pyšek 1998). Many species within this family present achene dimorphism (*i.e.* heterocarpy; Harper 1977), thus they produce two achene types, normally occupying a different location within the capitulum (the periphery or the center), and with different morphology, germination requirements or dispersal ability (Venable 1985; Sorensen 1978). Central ones are generally smaller, lighter and present pappus, beak or appendage structures that allow anemochorous dispersal, whereas peripheral ones are larger, heavier and lack of specific dispersal structures (Kigel 1992; Imbert 2002) but often include modifications that make them suitable to suffer passive-zoochory (Sorensen 1978) or hydrochory (Kigel 1992) dispersion. Thus, although usually considered anemochorous, these species can also be dispersed by other agents (polydispersal syndrome *sensu* Mossman 2009), combining different strategies to spread and reach new areas (Venable and Lawlor 1980). Therefore, polydispersal syndrome entails a wider range of environmental conditions under which these species can successfully germinate and establish (Harper 1977; Flint and Palmblad 1978; Imbert et al. 1997).

A large proportion of alien species originated in the Mediterranean Basin were introduced in Chile associated to the Spanish conquest of Latin America and became naturalized in the Mediterranean region of this country (Martín-Forés et al. 2012). Asteraceae is one of the best represented families at country scale

(13.9%) among the exotic herbaceous species described in central Chile (Martín-Forés et al. 2012). One of them is *Leontodon taraxacoides* (Vill.) Mérat. subsp. *longirostris* Finch & P.D. Sell (synonym: *Leontodon saxatilis* Lam. subsp. *rothii* Maire), common in Spain (its native range) although widely naturalized in Chile (the exotic range), as well as in other Mediterranean region as California (DiTomaso and Healy 2007) and Australia (Groves et al. 2003). *L. taraxacoides* constitutes the ideal candidate for this study because of its wide distribution range and because it produces two morphologically distinct achenes, dark brown heavy achenes without a pappus lying in one row at the edge of the capitulum and enclosed in the involucral bracts (peripheral achenes) and light brown inner ones with a pappus (central achenes).

The main aim of this study is to analyze differences in seed output per plant and achene dimorphism pattern associated to the colonization strategy of *L. taraxacoides* grown in common garden conditions in its Spanish source and Chilean recipient areas. To that end, we assess whether reproductive and dispersal-related traits vary depending on the common garden emplacement and the origin of the source population (country of origin) or precise collection site. Specifically, we hypothesize that the seed output and the central/peripheral ratio of achenes per capitulum will be higher for individuals from Chilean origin and individuals grown in the exotic range than for those coming from Spain and grown in the native range, respectively, to enhance anemochorous dispersion, which constitutes the main strategy to efficiently spread.

MATERIAL AND METHODS

Study area

The study was conducted in Mediterranean grasslands of Chile and Spain. In Chile, populations of *L. taraxacoides* were collected in the central region of Chile (from 32°31' to 37°00' S and 70°46' to 72°34' W), with mean annual precipitation ranging between 300-1200 mm. In Spain, the studied populations were collected in the center-west of the Iberian Peninsula (from 37°51' to 40°14' N and from 4°23' to 7°02' W), with mean annual precipitation ranging between 400-1100 mm (Fig. 31). Both regions are similar in terms of lithology (acid substrate, derived from igneous or metamorphic rocks), plant physiognomy (the structure consists on a continuous herbaceous layer with scattered trees), and land use (mainly extensive livestock grazing by sheep and cattle). Almost half (49%) of the species present in the Mediterranean Chilean grasslands are exotics originated mainly in the Mediterranean Basin (Martín-Forés et al. 2012), and fundamentally from the Iberian Peninsula (Groves 1986). These similarities can be explained by the climate and the historical-cultural context shared by Chile and Spain (Aronson et al. 1998; Arroyo et al. 2000; Figueroa et al. 2004).

Plant material and growing conditions

We selected *L. taraxacoides* for being a species typical from grasslands, originated in the Mediterranean Basin, and widely distributed along the Mediterranean type climates in both the source (Spain) and recipient (Chile) area. Selected sampling sites were representative of the whole rainfall gradient existing in each study area. Five sites were considered in Spain, and four in Chile (*L. taraxacoides* was not found in the driest Chilean site) (Fig. 31; Table 14). In spring of 2010 (May and June in Spanish sites, and October and November in Chilean ones) we collected mature capitula from 50 individuals of this species in each sampled site. Geographic coordinates and climate conditions, including annual precipitation, mean annual temperature, and the number of months with drought period or water deficit per year were determined at each site (Table 14). Climatic

data were obtained from the State Meteorological Agency (AEMET, http://www.aemet.es) and the Atlas Climático Digital de la Península Ibérica (Ninyerola et al. 2005) in Spain, and from WorldClim (Hijmans et al. 2005) in Chile, and the number of months with drought period was calculated by the method proposed by Bagnouls and Gaussen (1953).

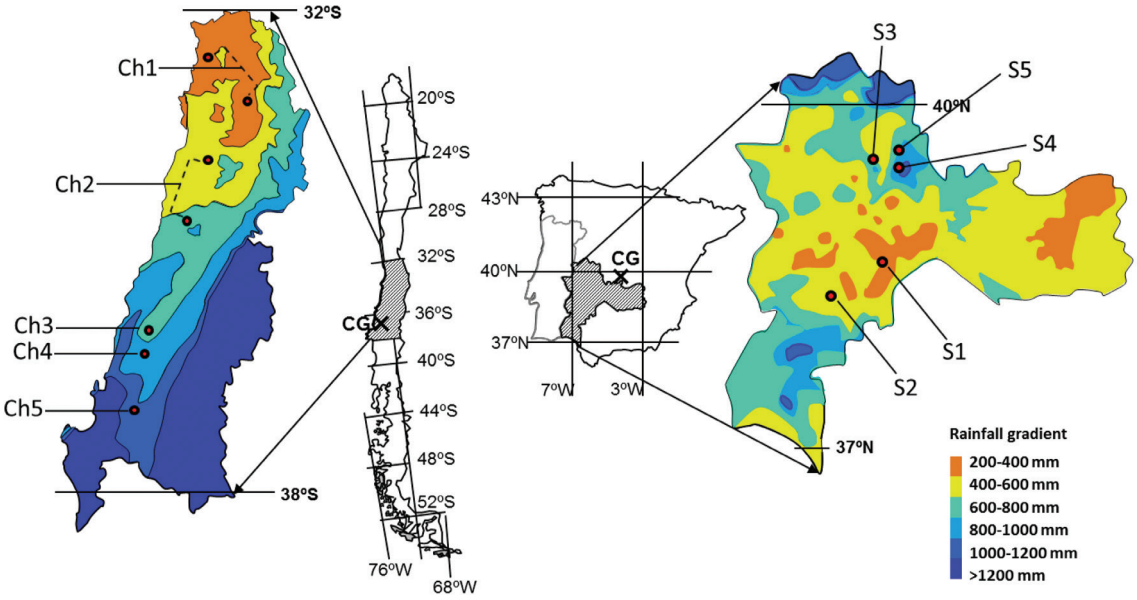

Fig. 31 Map of the studied areas of Mediterranean grasslands in Spain and Chile, including sampling sites (see Table 14). Grey tones represent rainfall variability in each country

Table 14. Geographic and climatic characteristics of the studied populations. TMED is mean annual temperature; PREC is annual precipitation, and MWD the number of months with drought period or water deficit per year.

Site	Country	Code	Latitude	Longitude	TMED (°C)	PREC (mm)	MWD
Pumanque	Chile	Ch2	34°37'48"S	71°42'54"W	15.01	719	5
Boldo	Chile	Ch3	35°58'52"S	72°13'38"W	14.33	794	5
Quirihue II	Chile	Ch4	36°15'20"S	72°32'58"W	13.14	972	5
Yumbel	Chile	Ch5	37°00'26"S	72°34'01"W	13.33	1168	4
Castuera	Spain	S1	38°46'20"N	5°34'48"W	16.89	468	4
Fuente de Canto	Spain	S2	38°16'33"N	6°20'22"W	15.81	572	4
Madroñera	Spain	S3	39°25'23"N	5°47'48"W	15.42	666	4
Ibor	Spain	S4	39°32'53"N	5°22'57"W	14.46	859	4
Logrosán	Spain	S5	39°21'28"N	5°25'04"W	16.17	913	3

Contaminants associated to collected capitula were removed in the lab to obtain clean achenes. Among them, peripheral achenes of *L. taraxacoides* were selected for being more successful in pre-germination studies, agreeing with previous literature (Imbert 1999, 2002; Brändel 2007). Seeds from each collection site were pre-germinated in petri dishes, and then transplanted to microplots in two common gardens (CG): the Experimental Center of Cauquenes-INIA, Chile (35°58' S, 72°17' W; 140 m a.s.l.) and the Faculty of Agronomy of the

Polytechnic University of Madrid, Spain (40º26'N, 3º44'W; 600 m a.s.l.). Plant establishment in field was conducted in June and October of 2012, respectively.

In each CG, three replicates were used per population, which were randomly assigned to microplots, getting a total of 15 microplots in Madrid and 12 (because of the absence of this species in the driest Chilean site) in Cauquenes. Ten and 20 individuals were arranged per microplot in Cauquenes and Madrid, respectively. Each microplot occupied an area of 50x100 cm in Cauquenes and 50x200 cm in Madrid. Individuals were separated 20 cm between them, whereas the separation between microplots was at least 30 cm. The total number of individuals planted was 270 in Cauquenes, and 540 in Madrid. However, throughout the experiment 39% (Cauquenes) and 55% (Madrid) of individuals died, so that finally 166 and 245 individuals were, respectively, assessed.

Data collection

Once the plants reached about 50% senescence, five capitula were collected from each individual and yield traits associated with reproductive effort and the invasive ability were studied. Total number of achenes per capitulum (AC) was counted, as well as the number of central achenes (with pappus) and peripheral ones (without a pappus). The proportion between central and peripheral achenes (C/P) was calculated for each capitulum. Values obtained for the five capitula were averaged to obtain the mean values per individual. When plants reached 75% of senescence they were harvested. Dried weight of aerial biomass and number of capitula per plant (CP) were measured. Seed output per plant (SEED) corresponds to the total number of seed and was calculated as CP x AC. Therefore, SEED and C/P were the response variables considered in this study which will reflect the colonization ability of *L. taraxacoides*.

Data analyses

We used regression trees to analyze the colonization ability considering differences in SEED per plant and achene dimorphism strategy (C/P) between populations. Explanatory variables included the common garden emplacement (CG, with two categories: Cauquenes and Madrid) and the origin of the source population, either at regional or a local scale: country of origin (ORIGIN, with two categories: Spain and Chile) and collection site (SITE, with nine categories), respectively. Regression tree is a nonparametric technique suitable for analyzing complex ecological data enabling the importance of the predictors considered to be hierarchized. Data are split into increasingly homogenous groups based on the predictor variable at each split that explains the greatest deviance of the data set. This analysis does not have assumptions regarding data distribution and it is robust in relation to outliers and missing data (De'ath and Fabricius 2000). Despite this, for each collection site, extreme atypical values that exceeded three times the interquartile range were removed prior to the analyses in order to diminish the number of outliers. We performed regression trees with SPSS 22 (IBM SPSS Statistics: Armonk, NY, USA) and used CHAID as the growing method, and a minimum number of cases in parental node of 50 and 10 in each subsidiary node.

To explore how plant performance influences SEED regression tests were conducted between biomass and the yield parameters CP, AC, and SEED. Additionally, to explore the dispersal strategy, and to assess whether the number of central or peripheral achenes is limited by the capitulum size, regression tests were carried out between number of achenes of each type and AC. All regression tests were performed separately for each of

the four groups resulting from grouping individuals by CG and ORIGIN. Comparison tests among the four regression slopes were carried out with Statgraphics Centurion XVI.II (Statgraphics Centurion XVI 2013) to assess whether significant differences exist in trends between groups.

Finally, we conducted Kruskal-Wallis tests to assess whether there were differences for biomass and AC among the four groups formed by the combination of CG and ORIGIN.

RESULTS

The main factor determining seed output per individual was CG emplacement whereas the proportion between types of achenes was controlled mainly by the country of origin of the populations (Fig. 32a). SEED was much higher in plants grown in the non-native environment (Cauquenes) but, within Cauquenes CG, individuals from Spanish populations exhibited significantly higher values than those from Chilean ones. Nevertheless, plants from Chilean populations produced higher proportion of central achenes (higher C/P values) than those plants from Spanish origin (Fig. 32b). Within each ORIGIN, C/P was always higher for the populations grown in the colonized range (Cauquenes) than in the native one (Madrid). In the two response variables, some variability of minor importance was also obtained associated with SITE but it did not seem to follow a pattern related to annual precipitation of the sampled sites, so it might be related to other abiotic conditions occurring at local scale.

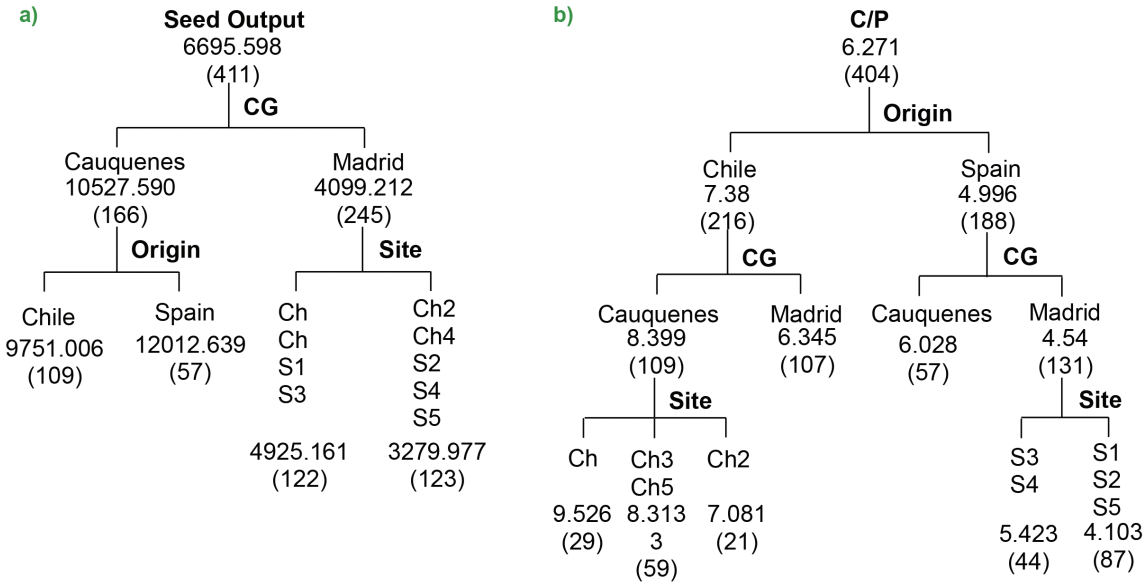

Fig. 32 Regression trees for seed output per plant (a) and central/peripheral achenes ratio (C/P) (b), classified according to common garden emplacement (CG), country of origin of seeds, and site where the source population originated. Values under each final node are average values of each parameter for cases within that group, while values in brackets represent the number of cases for that group. Signification level considered was $p < 0.05$

SEED and yield components —CP and AC— of populations were positive and significantly correlated with plant biomass (Fig. 33). Those trends were observed for the four groups of populations considered, with the exception of the relationship obtained for AC in Spanish and Chilean populations grown in Cauquenes (Fig. 33c). The differences in the slopes of the regressions between biomass and both seed output and number

of capitula were not significant except for Chilean populations grown in Madrid (Table 15). In the case of number of achenes per capitulum its variation associated with biomass were ten times higher in Madrid than in Cauquenes, independently of the country of origin of populations.

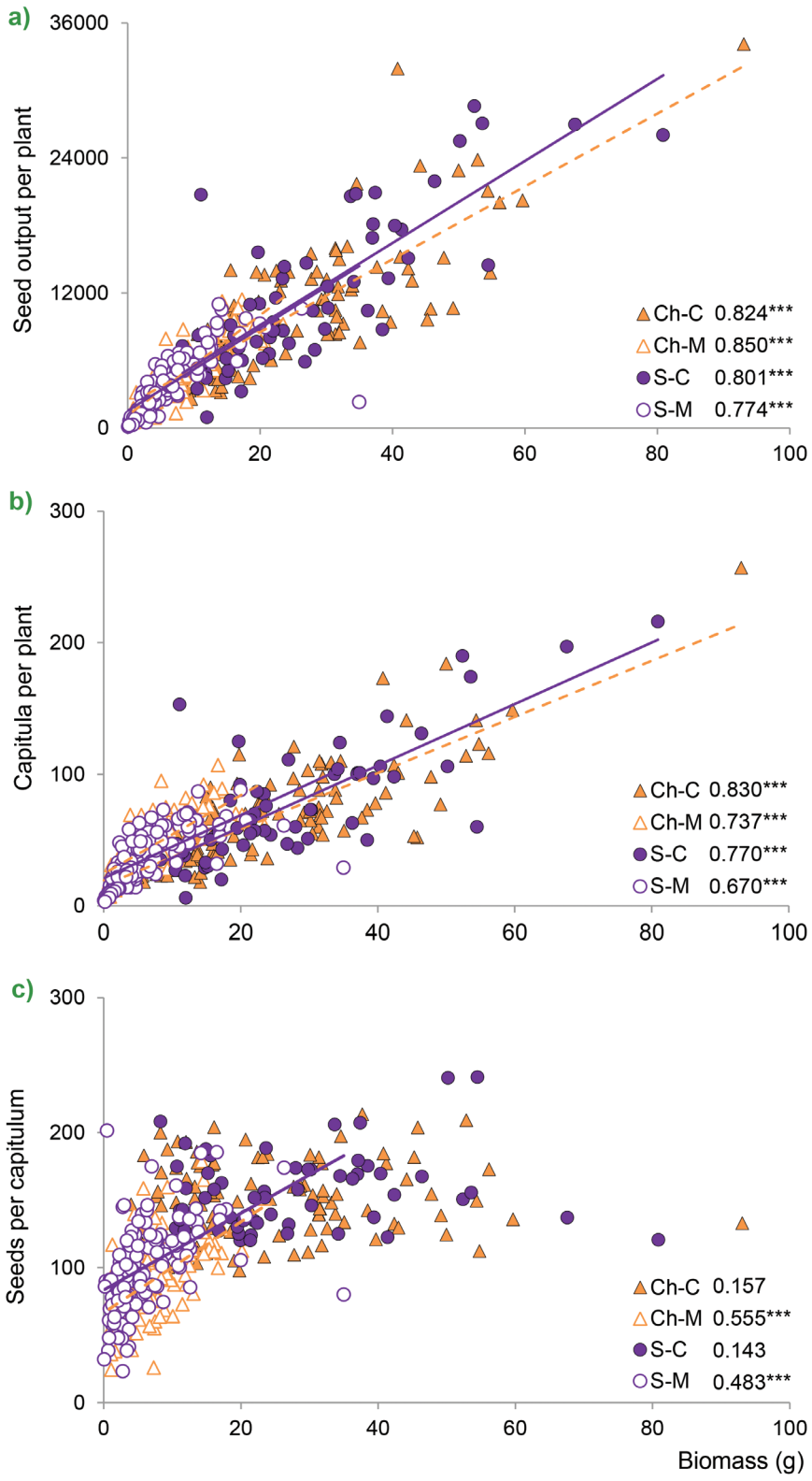

Fig. 33 Regression between biomass and seed output per plant (a), number of capitula per plant (b), and number of seeds per capitulum (c). Close symbols correspond to Cauquenes (C) common garden whereas open ones refer to Madrid (M) common garden. Circles represent populations from Spain (S) whereas triangles are populations from Chile (Ch). Significant relationships are shown by discontinuous (Chilean populations) or continuous (Spanish populations) lines. For each relationship, Pearson correlation coefficient and its significance (* < 0.05; ** <0.01; *** < 0.001) are shown

Table 15. Slopes obtained in the regression tests conducted between biomass and yield components, and between number of achenes per capitulum (AC) and number of peripheral and central achenes. Regressions were grouped by combining common garden emplacement and country of origin (see Fig. 33 and 34). Different letters indicate significant differences ($p > 0.05$) obtained in the pairs comparison of slopes.

		Common Garden			
		Cauquenes		Madrid	
		Chilean sites	Spanish sites	Chilean sites	Spanish sites
Biomass	Seed output	323.61 a	364.46 ab	446.13 b	367.48 a
	Capitula/plant	2.13 a	2.34 ab	2.98 b	2.40 ab
	Achenes/capitulum	0.30 b	0.27 b	3.37 a	2.84 a
AC	Central achenes	0.93 a	0.89 a	0.90 a	0.89 a
	Peripheral achenes	0.07 a	0.10 a	0.08 a	0.11 a

Both central and peripheral achenes increased with number of achenes per capitulum, in populations from both countries grown in the native and the non-native environments (Fig. 34a, b). That trend was especially noticeable in the case of central achenes, with correlation coefficients above 0.9 in all cases, while for peripheral ones the trend was less pronounced (correlation coefficients ranged from 0.2 to 0.7). No significant differences were found in the regression slopes when comparing the four groups resulting from the combination of CG and country of origin (Table 15).

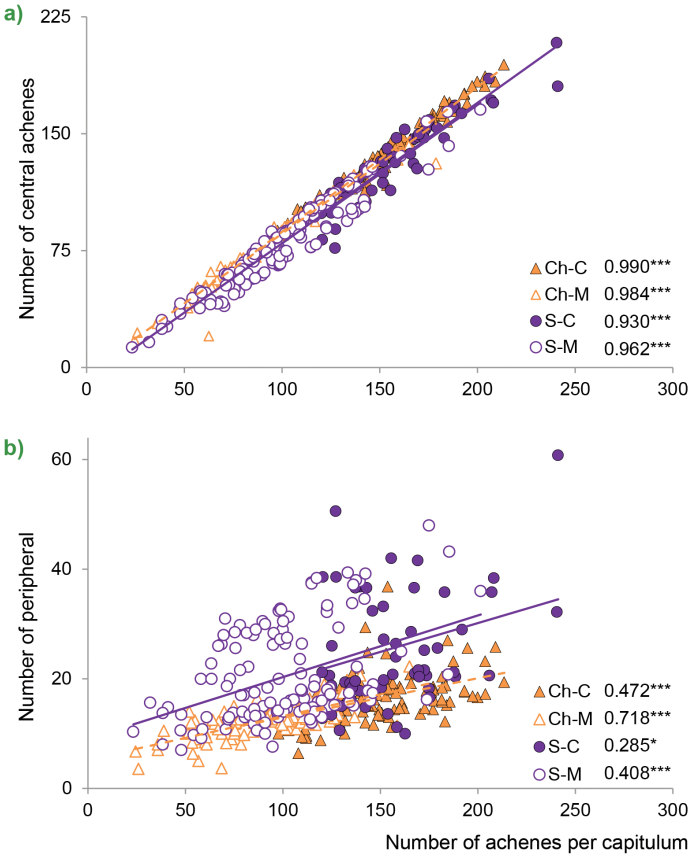

Fig. 34 Regression between number of central (a) and peripheral (b) achenes and number of seeds per capitulum. Close symbols are employed for peripheral achenes whereas open ones refer to central ones. Close symbols correspond to Cauquenes (C) common garden whereas open ones refer to Madrid (M) common garden. Circles represent populations from Spain (S) whereas triangles are populations from Chile (Ch). Significant relationships are shown by discontinuous (Chilean populations) or continuous (Spanish populations) lines. For each relationship, Pearson correlation coefficient and its significance (* < 0.05; ** <0.01; *** < 0.001) are shown

Significant differences in biomass (Fig. 35a; Kruskal-Wallis test, $p < 0.0001$) and number of achenes per capitulum (Fig. 35b; Kruskal-Wallis test, $p < 0.0001$) were found between CGs. Within each CG, no significant differences were found regarding the origin of the population.

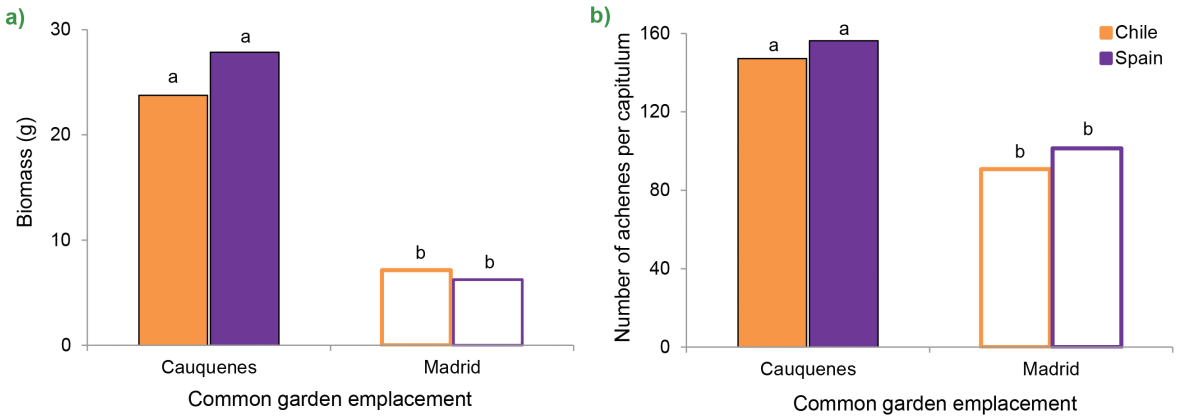

Fig. 35 Histograms for values of biomass (a) and number of achenes per capitulum (b) grouped by common garden and country of origin of populations. Different letters indicate significant differences among groups according to the Kruskal-Wallis tests and post-hoc pair comparisons

DISCUSSION

Our results show that *L. taraxacoides* combines different adaptive strategies acting conjunctively on seed output and type of achene production, in order to maximize the colonization ability and efficiency of this species.

The 'residence time hypothesis' propose that the longer since exotic species arrival to the non-native area, the more chances of being a successful colonizer (Pyšek et al. 2004; Hamilton et al. 2005). Introduction of *L. taraxacoides* in Chile dates back to the last decades; its first record as introduced in this country was in 1963 (Castro 2005), so according to its short residence time, it would be expected a narrow regional distribution of this species in Chile (Arroyo et al. 2000; Pauchard et al. 2004; Castro et al. 2005). However it has become widely distributed and is currently present in several administrative regions (from approx. latitude 32 to 42 °S, *i.e.* beyond the Mediterranean area; Fuentes et al. 2013). Moreover, it is the most frequent alien species in the country (Martín-Forés et al. 2012), which reveals the success in the colonization of *L. taraxacoides*, overcoming the new conditions and abiotic filters (Martín-Forés et al. 2015). The main factor that determines its spatial distribution is anthropogenic activities (Dainese and Poldini 2012). Thus, the colonization ability of this species is submitted mostly to its capacity to colonize empty niches, coping to the novel conditions created after human disturbance ('novel niche hypothesis', Shea and Chesson 2002) and its dispersal ability (related to the 'propagule pressure hypothesis', Lockwood et al. 2005).

Once *L. taraxacoides* arrives to the colonized range, to survive in the novel conditions created it has followed the low risk/high risk strategy (Venable et al. 1987; Venable and Brown 1988). As anemochorous spreading is subjugated to stochastic events (seeds loss often occurs due to the high probability of falling in unfavorable sites), heterocarpy in Asteraceae constitutes an important mechanism to enhance colonization. Peripheral achenes in *L. taraxacoides* have higher size, thicker pericarp and longer viability duration (Priestley 1986; Baker 1989) than central ones. They lack structures for anemochorous dispersal achieving a self-replacement strategy (McEvoy 1984), thus, plants originated from these achenes should be able to colonize the niche where the mother plant grew (Imbert 1999; Brändel 2007) and adapt to the local novel conditions (Brändel 2007). In this way,

the sway of stochastic events during dispersal decreases (Imbert 1999) and the chance of getting naturalized in the vicinity of the mother plant increases, accomplishing the challenges related to the novel niche hypothesis. On the contrary, central achenes with anemochorious dispersion achieve long distance dispersal events reaching further areas (Venable et al. 1997; Brändel 2007). They are always larger in number and spread further than peripheral ones, enhancing propagule pressure in the areas they reach, and consequently trying to expand the area of distribution of the species, accomplishing the challenges related to the propagule pressure hypothesis.

Phenotypic plasticity (Sultan 2000) and ecotypic differentiation (Lortie and Aarssen 1996) are key mechanisms to cope to the challenges associated to the colonization process. In this sense, *L. taraxacoides* shows a combination of these two strategies regarding both seed output per individual and achene dimorphism patterns. Our results indicate that the main adaptation mechanism for seed output is phenotypic plasticity, showing higher production under the common garden conditions of the exotic range. Number of seed produced per individual and is highly dependent on the aerial biomass. Biomass production is invested in reproductive effort, enhancing the two parameters involved in seed output: number of capitula and number of achenes per capitulum. Both parameters increase with biomass, but in the case of the number of achenes per capitulum there is an asymptotic response, indicating an architectonic constriction: the receptacle (*e.g.* the surface of the capitulum where the seed are implanted) can increase but only up to a limit associated to each species. Biomass as predictor of seed production has shown great phenotypic plasticity, reaching significantly higher values for individuals grown in the exotic range **(Fig. 35a)**. This trend to bigger individual in exotic range is a common feature for many exotic species (see for example Maron et al. 2007; Kumschick et al. 2013; Leishman et al. 2014), constituting an effective strategy to produce more dispersal units and promote the species colonization ability.

In contrast, achene dimorphism production presents typically ecotypic differentiation (as occurs in Crepis sancta; Imbert 2001), and to a lesser extent also phenotypic plasticity. Central/peripheral ratio is mostly determined by the country of origin of populations (suggesting ecotypic variations) being C/P 1.5 times greater in Chilean populations than in Spanish ones. Within each country of origin individuals growing in the exotic range also increases this ratio, indicating some phenotypic plasticity. Higher proportion of anemochorous central achenes is a strategy to maximize seed spreading in the colonized area, thus the 'invasive ability' seems to appear enhanced in the exotic range of the species (Kumschick et al. 2013). Similarly, both number of central and peripheral achenes increase with the number of achenes per capitulum in plants coming from populations of the two countries and the two common gardens. However, for central achenes the relationship is stricter ($R^2 > 0.9$ in all cases) and the regression slope is one order of magnitude higher than the relationship for peripheral ones. Considering the number of achenes per capitulum as a surrogate of the capitulum size, this differential performance could be due to an architectural constriction. In this sense, when the radius of the receptacle increases, the number of peripheral achenes (arranged in one row at the edge in the involucral bracts) increases according to the length of the circumference whereas the number of central ones increases according to the surface area of the receptacle; therefore, the capitulum's carrying capacity differs for each type of achenes. As the number of achenes per capitulum is significantly higher for populations grown in the non-native environment, it reverts to produce proportionally more central achenes in the colonized area.

In summary, maximizing colonization ability is a key strategy for alien invasive species. In this sense, some alien plant species such as *L. taraxacoides* combine phenotypic plasticity and ecotypic differentiation as coadaptations to the novel conditions and as a strategy to increase propagule pressure and spreading in the new environment. For this reason, it is crucial to include the assessment of both adaptations in biological

invasion studies and conservation strategies. *L. taraxacoides* does not require complex mechanisms to increase its capacity of expansion: simple architectural relationships (number and size of capitula) largely dependent on biomass and different dispersal strategies can enhance the successful adaptation and spreading in its invaded range. Regarding this, alien species with achene dimorphism should be carefully controlled and their spreading consciously monitored. Asteraceae family in a broad sense and *L. taraxacoides* particularly are of special concern due to its invasive potential.

Discussion

The infinite vibratory levels, the dimensions of interconnectedness are without end. There is nothing independent. All beings and things are residents in your awareness.

Alex Grey

DISCUSSION

The introduction of an agro-silvopastoral system associated to the Spaniards' conquest in the Mediterranean region of Chile involved the establishment of disturbance regimes that favored the entry of alien species (Le Houérou 1991; Holmgren et al. 2000). Due to the historical-cultural context of the colonialism (National Geographic Society 1991), the Mediterranean Basin, especially the Iberian Peninsula, has constituted the main source area donor of exotic flora to Latin America, and particularly to central Chile which constitutes the main recipient area where the exotic flora has been established. In this study, we found a great floristic parallelism between Spain and Chile, particularly when comparing the agro-forestry systems of the Mediterranean regions of both countries. The Chilean agroecosystem, *espinal*, represents to a large extent a replication, in terms of physiognomy and function, of the Spanish's agricultural model, *dehesa* (Ovalle and Avendaño 1987; Ovalle et al. 1990). As a result of the introduction of the agrarian culture in central Chile, including the management of the system (fallow, rotation) and technology (plowing, harrowing, and animal traction) used in the Mediterranean Basin, animal and plant species (livestock, cereals and associated weeds) were also introduced.

Chilean population is concentrated primarily in central Chile due to the environmental conditions of that area. Associated to human presence, land use changes have occurred including agriculture intensification (Montenegro et al. 1991), urbanization (Pauchard et al. 2006), and network road connectivity (Arroyo et al. 2000). This area, despite representing only the 20% of the country's territory, holds a high concentration (80% of all the country's exotic plants) of naturalized plants (Matthei, 1995) and people (78% of the country's population; Pauchard et al. 2006; INE 2007).

The representation of the alien flora becomes greater (Gaertner et al. 2009) at more detailed spatial scales: 12% in continental Chile, reaching 20% in central Chile, and rising up to 49% when considering the *espinales*. This percentage of aliens in the *espinal* reaches almost half of the flora it contains, being most of the exotic species annuals (84%) from Eurasian origin (97%).

As a result of the landscape transformation by humans in Chile, empty niches were created. That has constituted an opportunity window (Tilman 1997; Zobel et al. 2000) for the entry of alien species (Le Houérou 1991; Holmgren et al. 2000; Jauni et al. 2015) which have already been adapted to disturbances and cultural landscapes (Prinzing et al. 2002; Arianoutsou et al. 2013) in their region of origin for millennia (eco-evolutionary experience; Saul et al. 2013). The long-term coexistence of Mediterranean pastures with anthropic management has determined processes of co-evolution between plants and human practices (Di Castri 1981; Pineda and Montalvo 1995; Holmgren 2002; Ricotta et al. 2009; HilleRisLambers et al. 2010), so plants presenting more competitive traits in a context of livestock grazing and plowing have become selected (De Miguel et al. 2010). On the contrary, original flora from the Chilean Mediterranean region lacked adaptations to continuous grazing and other natural disturbances, thus native species have resulted negatively affected with the introduction of livestock and crops which has favored aliens' establishment (Milchunas and Lauenroth 1993; Holmgren et al. 2000; del Pozo et al. 2006; Ovalle et al. 2006; Díaz et al. 2007).

Among the alien flora present in Chile, the families most represented are Poaceae, Asteraceae and Fabaceae, in accordance with the three most invasive families worldwide (Pyšek 1998). The rapid growth and high reproduction rates of annual plant species, and their capacity to resist unfavorable periods in the form of seeds makes them more suitable to develop in disturbed open spaces by fire, plowing or grazing (Le Floc'h 1991;

Gómez-González et al. 2010). Poaceae and Fabaceae are typical families associated to livestock grazing and crop cultivation practices. By their part, Asteraceae species take advantage in spreading mechanisms. They usually present achene dimorphism production, yielding two achene types (occupying either the periphery or the centre of the capitulum; Imbert 1999) with different morphology and dispersal ability (Venable 1985).

Species' strategy to adapt to the new environmental conditions is dependent on the family, as well as on the origin (source or recipient area) of the population considered. Populations collected in the source area show more ecotypic differentiation while phenotypic plasticity appears to be higher for populations from the recipient area. Regarding the species' family, Fabaceae, such as *Medicago polymorpha* (del Pozo et al. 2000, 2002a, b) and *Trifolium glomeratum* rely predominately on ecotypic differentiation mechanism, showing a delay in plant development with higher values of mean annual precipitation in their region of origin (it reflects an adaptation to their original environmental conditions, giving plants more time to invest on biomass and fruit production in a more favorable environment). On the contrary, Asteraceae such as *L. taraxacoides* shows greater plasticity which may be related with its polydispersal syndrome (central achenes with pappus achieving long distance dispersal events by anemochory, and peripheral achenes including modifications to suffer passive-zoochory).

The eco-evolutionary experience of plant populations also influences the main mechanism of adaptation that species rely on to face the new conditions of the non-native environment. While Spanish populations have had more time to develop new ecotypes and genetic differentiations, exotic plants recently established in Chile, although with large variation on their time since arrival (Castro et al. 2005; Fuentes et al. 2013), did not have that chance. For example, *L. taraxacoides* is the most frequent alien species in central Chile although it was recently introduced in this country (first record in 1963; Castro, 2005). Contrarily to what it might be expected due to its short residence time (Parker et al. 2003; Richardson and Pyšek, 2012), this species is widely distributed due to its invasive character (*sensu* Richardson 2000). Its success in colonization is owing to an extraordinary combination of coadaptive mechanisms (ecotypic differentiation and phenotypic plasticity) that allows this species facing the new environmental conditions (Maron et al. 2004, 2007) by enhancing its survival, plant development, propagule pressure, and spreading. On account of the short residence time of *L. taraxacoides* in Chile, its spatial distribution is mainly determined by anthropogenic factors (Dainese and Poldini 2012). Thus, the colonization ability of this species is submitted mostly to its capacity to colonize empty niches, coping to the novel conditions created after human disturbance ('novel niche hypothesis'; Shea and Chesson 2002) and its dispersal ability (related to the 'propagule pressure hypothesis'; Lockwood et al. 2005). As Chilean populations of *L. taraxacoides* were possibly originated from few populations of Mediterranean Basin (therefore with low genetic diversity), and they have to become adapted to the whole Chilean climatic gradient, greater phenotypic plasticity seem a successful adaptive mechanism to acclimatize to changing environmental conditions (supported by Geng et al. 2007; Dostál et al. 2012 and Gratani 2014). To cope with these novel conditions, *L. taraxacoides* follows the low risk/high risk strategy (Venable et al. 1987; Venable and Brown 1988); its peripheral achenes produced adhere to the self-replacement strategy (McEvoy 1984), getting naturalized in the vicinity of the mother plant (Imbert 1999). However, central achenes presenting anemochory are more numerous and spread further, enhancing propagule pressure in the long distance to try to expand the area of distribution of the species. For all this, *L. taraxacoides* constitutes a faithful reflection of the colonization process in Chile.

Despite the similarities between the *dehesa* and the *espinal*, there are also differences between these two agroecosystems, especially regarding species richness (much higher in Spain); hence *espinales* seem to constitute a system equivalent to the Spanish *dehesas* although with lower biodiversity levels. It is known that

the number of alien species becoming established in a colonized area is lower than the amount that might potentially arrive (Malo and Suárez 1997), but in Chile less than the 10% –assuming the tens rule of Williamson (1996)– are currently naturalized. This could be due to the fact that alien species were not able to leave the source area, failed in transport pathway, or failed to establish and persist in the recipient area. Thus, there are also some factors conditioning, filtering and restricting this naturalization process acting either in the source and/or in the recipient area. Previous studies attempted to determine whether the factors that best determine level of invasion are climatic ones (Weiher and Keddy 1999; Gaston et al. 2003; Thuiller et al. 2005; Wiens and Graham 2005; Kueffer et al. 2010) or those related to the habitat's characteristics (Hejda et al. 2009; Jansen et al. 2011; Dostál et al. 2013; Kalusová et al. 2013; Marini et al. 2013). Our results indicate that both factors act conjunctively and in a hierarchical manner at different scales.

At a broad scale (*i.e.* continental), climate determines the possibilities of alien establishment; our results bring to the light the significant biogeographical association between the climates in the regions of origin (considering here all the possible continents) and destination (*i.e.* geographic Chilean regions) of exotic species present in Chile. The similarity between the climate of the source and the recipient areas plays a crucial role (Alpert et al. 2000; Davis et al. 2000; Chytrý et al. 2008, 2009) in the current distribution of exotic species in Chile. The species' climatic tolerance is essential to successfully establish in the new region (Haider et al. 2010), which highlights the importance of coadaptive mechanisms, but mainly plasticity in overcoming environmental barriers. The habitat characteristics of the source area (climate, soil nutrient status, propagule pressure, disturbance, and remarkably human activities) determine the communities' potential to act as main donors of alien species to Chile. However, the relative importance of those factors ultimately depends upon the climate of the recipient Chilean climatic region and the distribution of the main land uses throughout the country, highlighting the importance of human pressure as a driver of alien distribution in the recipient area (Marini et al. 2012).

When analyzing the abiotic filters (climate- and edaphic-related) at a finer scale (Spanish *dehesas* and Chilean *espinales*) we found the existence of filtering process acting in both the source and the recipient areas but with different intensity. The influence of abiotic factors is stronger in the recipient area, where especially the climate determines the successful naturalization of alien species in Chile, agreeing with previous reports about invasibility (Kolar and Lodge 2001; Dawson et al. 2009; González-Moreno et al. 2014). In Chile, alien species richness increases with precipitation and with the shortening of summer drought period, which supports the 'resource availability hypothesis' (Davis et al. 2000; Richardson and Pyšek 2006), being naturalization enhanced by an improvement in the main limiting resource (water) (Cleland et al. 2004; Kreyling et al. 2008).

In the recipient area, not only abiotic filters but also biotic ones can be acting, for example, along the processes of plant community structuring and ontogeny (Armas and Pugnaire 2005; Armas et al. 2013; Jeffers et al. 2015). Contrarily to recent studies (Kulmatiski 2006; Vilà et al. 2011; Tognetti and Chaneton 2012) stating that alien species established in early successional stages impede the re-establishment of native ones, our results show no apparent competition between alien species and Chilean native ones along secondary succession. Rather, the results suggest that they play a complementary role: there is a segregation of niches between both species groups occurring at local scale in earlier stages of succession. Whereas time since cultivation abandonment has a positive effect on native species richness, alien species increase after the first years of abandonment but then remain stable until the end of the chronosequence (contrary to Meiners et al. 2002; Tognetti et al. 2010). The increase in vegetation cover associated with the early colonization by aliens seems to create the appropriate conditions for the arrival of native species which increment in number. Thus, aliens act like passengers (Macdougall and

Turkington 2005) or even tolerants and/or facilitators playing a complementary role to the natives' one. This coexistence under the conditions of extensive livestock grazing is achieved through two different strategies: alien species are mainly grazing-tolerant whereas native species are grazing-defensive species.

Although many studies have indicated a similar role of native and alien species in structuring communities along secondary succession (Meiners 2007; Tognetti et al. 2010; McLane et al. 2012), our results indicate that the behavior of the species depends on their geographical origin. Structured plant communities are higher than the expected from random in both agrosilvopastoral systems, *dehesas* and *espinales*. Nevertheless, when comparing patterns of species' segregation for the colonizer species and the ones exclusive to each country, the source and the recipient areas differ in the community structure. Spatial segregation is clearer for species exclusive to Spain than for those exclusive to Chile, which may be due to the eco-evolutionary history that gave Spanish populations more time to become greater organized. However, the trend is reversed in the case of colonizer species, which show a greater segregation in Chile than in Spain, possibly due to the environmental heterogeneity and the role played by alien species in the process of plant community assembly occurred in the recipient area after a disturbance, more than be caused by processes of interspecific competition.

The above-exposed hierarchical influence of several abiotic and biotic factors on establishment and naturalization processes brings to the light that biological invasions are dependent on the context, the scale (Lloret et al. 2005; Guo et al. 2006; Pyšek and Richardson 2007), and the specific traits of the species studied. For example, when study three of the most abundant exotic species in Chile —*L. taraxacoides*, *Hypochaeris glabra* and *T. glomeratum*— plants survival vary depending on the origin of the population and the emplacement where plants grow, being higher for exotic populations and individuals grown in the non-native environment. Similarly, the invasive ability of *L. taraxacoides* also varies depending on the context; this species enhances biomass production, seed output, and spreading when grows in the invaded range (enhancement of the invasive ability in the exotic range of the species; Kumschick et al. 2013). Future outcomes can include the combination of the current ecological knowledge in invasion processes with forthcoming global change scenarios (Sala et al. 2000; Pineda et al. 2014). Merging the prospection of future climate change (IPCC 2014), landscape heterogeneity, land-use shifts, and the subsequent modelled displacement of exotic plant species' distribution with current knowledge on invasive processes will be a fruitful study for determining areas more prone to invasion. Habitat invasibility can be studied either focusing on climatic terms (as occurs with wetter sites in central Chile and the latitudinal displacement of its flora due to the dry conditions), on habitat alteration (Chytrý et al. 2008; Pyšek et al. 2009; Jansen et al. 2011; González-Moreno et al. 2014), as well as on areas that have a greater potential to act as donor of alien species (Dostál et al. 2013; Kalusová et al. 2013; Kalusová et al. 2014).

Evaluating the factors and determinants involve in naturalization and invasion processes is key to accomplish the objectives of the Millennium Ecosystem Assessment Program (MA 2005; Carpenter et al. 2009). The exchange of species, successful establishment of some of them or extinction of others, their effect in the native plant community and the consequences on the rest of species ligated somehow to the aliens' presence undoubtedly contributes to the emergence of new environmental scenarios. These new scenarios have ecological and socioeconomic repercussions that are difficult to evaluate short-term (Rockstrom et al. 2009) or at a determined spatial scale. As multi-scale patterns are determinant of naturalization success, evaluations should be conducted from broader to finer geographical scales, and in the short, medium and especially long term (Strayer et al. 2006; Lankau et al. 2009). We appeal for the importance of identifying not only changes in ecosystem structure and functioning as a consequence of the species' naturalization, but also conduct *a priori* evaluations

to understand these processes. To that end, we should take a comprehensive and systemic approach, coming to understand that fundamental ecology is context-dependent, being tightly bound up to the social-cultural history, the anthropic activity, the economic implications, and the social tradeoffs (Pejchar and Mooney 2009). Thus, it is necessary to accomplish transdisciplinary decision-making processes (Seastedt et al. 2006; Díaz et al. 2015) which take into account not only ecological consequences, but also ecosystem services and human well-being (Bennett et al. 2015), where different scientific experts and stakeholders are involved (Mace 2014; Martín-López and Montes 2015; Pineda et al. 2015; Velasco et al. 2015).

Towards a new paradigm: neither good nor evil

All our results demonstrate that alien species coming from Spain are pre-adapted to the environmental conditions and land-use management in the new region (supported by Pyšek and Richardson 2007; Richardson and Pyšek 2012), and that once they get naturalized in that non-native environment, they form mixed native/exotic plant communities showing an effective coexistence between both species groups (maybe related to Chilean unsaturated plant communities; Gilbert and Lechowicz 2005). This coexistence does not seem to be aggressive, despite previous studies have suggested high competition by aliens (D'Antonio and Mahall 1991; Fogarty and Facelli 1999; Young et al. 2001) and in opposition to the traditional believe that aliens' naturalization always decreases native biodiversity (Richardson et al. 1989; Davis 2003) or displaces it by exclusion undertaking a process of global biological homogenization (McKinney and Lockwood 2001; Olden 2006; Olden and Rooney 2006; Winter et al. 2009). On the contrary, the coexistence between native and alien species in Chilean *espinales* appears pacific. It even suggests that some benefits or facilitation processes are occurring between native and exotic species. Aliens seem to ameliorate the harsh environmental conditions created after a disturbance so that natives can re-establish in that area. Previous studies reported an improvement of soil quality by the exotic species *Lantana camara* (Patel 2011), or even the fact that some exotic species can contribute to achieve native species conservation policies (Schlaepfer et al. 2011). In the foreseeable future it would be desirable to evaluate in detail possible facilitation processes between native and aliens by studying plant-plant interactions.

There is a publication bias towards studies focusing on biological invasions by exotic species as a harmful process with negative impacts (Davis et al. 2011), especially in ecological terms, whereas studies regarding the behavior of some invasive native species (Carey et al. 2012), or those focusing on the possible benefits that aliens can provide have been overlooked receiving much less attention (Rodríguez, 2006; Schlaepfer et al. 2011; Pienkowski et al. 2015). Although we are also aware of reports about serious negative impacts in ecology (Lowe et al. 2000; McGeoch et al. 2010), economy, (Pimentel et al. 2001, 2005) and society (Pejchar and Mooney 2009), we highlight the crucial importance of adopting a more balanced view of exotic species, understanding their presence in a new area as a holistic process (Schlaepfer et al. 2012). Conservation policies often suggest eradication of aliens, and the urgent need of monitoring, managing and implementing policies that control this 'problem' (Simberloff et al. 2005). However, being critical and enough open-minded to find any possible mutualistic interactions owing to the aliens' presence in an invaded range is crucial. Recent studies showed that certain invasive species have become keystones for the survival of local endemism and therefore eradication programs to re-establish the original vegetation might provoke severe population bottlenecks, local extinction of endemic species (Van Riel et al. 2000; Pienkowski et al. 2015), and cascading effects across trophic levels (Rodríguez 2006; Courchamp et al. 2001), or other ecosystem components (Zabaleta et al. 2001). It seems therefore that it is time to derogate the traditional paradigm which, by default, considers exotic species as an evil enemy because it is obsolete.

As W. Shakespeare said *"there is nothing either good or bad, but thinking makes it so"*. Thus, the consequences of the aliens' naturalization depend on the human perception of that process. Indeed, different stakeholders (García-Llorente et al. 2008, 2011) with different socio-cultural contexts have very different opinions about alien species; some of them recognize the benefits of exotic species not only on the native flora at local scale, but also on other species they have established relationships with (Van Riel et al. 2000), on the ecosystem services (Pejchar and Mooney 2009; Young 2010, 2012; Shackleton et al. 2011a), on the human wellbeing (Shackleton et al. 2006, 2011b), on the local and global economy (Pienkowski et al. 2015), etc. As an example, Chilean agronomists forming part of our research team are delighted with the naturalized leguminous species originated in Spain and the large sized exotic plants grown for agronomic purposes.

When most researchers study the naturalization process of exotic species they do not do it from an objective point of view, but by judging due to the negative predisposition to 'alien enemies' widely accepted even in the scientific community. However, when it concerns socio-cultural frame we consider new forms of mixture and cooperation among human beings as a sign of development, cooperation, and cultural enrichment. Maybe we should ask ourselves our reasons to not to take the same standpoint for plant communities. Instead of understanding the alien species as a catastrophic driver that causes negative impacts and landscape homogenization… why don't we shift the obsolete paradigm to a more inclusive approach that considers naturalization as a hybridization process? Why we keep using non-neutral terminology to refer to those non-indigenous species (Colautti and MacIsaac 2004)? Does making distinction between indigenous and non-indigenous species still make sense?

"The oldest and strongest emotion of mankind is fear, and the oldest and strongest kind of fear is fear of the unknown."

Howard Phillips Lovecraft

"Fear Is the Antithesis of Freedom"

Osho

"Man can learn nothing except by going from the known to the unknown"

Claude Bernard

Conclusiones
Conclusions

"Learn from yesterday, live for today, hope for tomorrow.
The important thing is not to stop questioning"

A. Eintein

CONCLUSIONES

1. La mayor parte de las plantas no nativas presentes Chile son especies anuales de origen euromediterráneo. Existe una correspondencia entre las regiones de origen de dichas especies no nativas y su ciclo biológico. Las plantas anuales proceden fundamentalmente de la Cuenca Mediterránea, mientras que las perennes son de origen africano y americano.

2. La flora de Chile central constituye una fiel expresión de la del conjunto del país en cuanto a porcentajes de las familias más representadas, tipo biológico y región de origen de las especies no nativas. Las familias más comunes dentro de la flora chilena no nativa son Poaceae, Asteraceae y Fabaceae, y la especie más abundante es *Leontodon taraxacoides* (Vill.) Mérat.

3. La proporción de la flora no nativa presente en Chile tiende a incrementarse a escalas de mayor detalle, siendo un 13% para el país en su totalidad, un 18% para la zona central, y alcanzando un 49% en los espinales. La distribución de familias, origen biogeográfico y carácter anual o perenne en los espinales es del mismo orden de magnitud que los encontrados en las dehesas españolas. Ambos sistemas agrosilvopastorales son equivalentes en términos florísticos, aunque la riqueza de especies es mayor en España.

4. El clima actúa como el principal predictor del potencial de establecimiento de las especies a gran escala. Existe una correspondencia entre las características climáticas de las comunidades en sus áreas de origen y de destino. Las comunidades relacionadas con hábitats con mayor influencia antrópica en el área de origen, como las ruderales y las procedentes de cultivos, actúan como principales donantes de especies, aunque la importancia de las características del hábitat depende del clima de la región de destino.

5. La colonización es dependiente del contexto y la escala de detalle, por lo que para su estudio es necesario considerar territorios que recojan una amplia heterogeneidad ambiental y diferentes escalas espaciales. La influencia jerárquica de los factores ambientales indica la existencia de filtros que seleccionan especies pre-adaptadas a las condiciones climáticas y de hábitat de la región de destino.

6. Los factores ambientales que afectan a la riqueza de especies son diferentes para las regiones mediterráneas de España y Chile. En España, las especies colonizadoras están ligeramente relacionadas con una combinación de factores climáticos y edáficos, mientras que en Chile el número de especies exóticas es altamente dependiente de las características climáticas, especialmente de la disponibilidad hídrica.

7. El hecho de que no exista relación entre la riqueza de especies nativas y exóticas a escala local indica que, en la naturalización transcontinental ocurrida en Chile, los filtros bióticos (es decir, la competencia entre especies) son menos importantes que los abióticos.

8. La segregación espacial de las especies en las comunidades españolas y chilenas es mayor que la que se esperaría por azar. Las especies se organizan como respuesta a los condicionantes climáticos y edáficos, pero este patrón se expresa con diferente intensidad en las dos regiones. Nuestros resultados destacan la existencia de diferencias inter-regionales en los patrones de co-ocurrencia de las especies colonizadoras y exclusivas. Las especies exclusivas presentan mayor segregación espacial en España, mientras que para las colonizadoras es más evidente en Chile. La combinación de los patrones de ambos grupos de especies en cada país condiciona la respuesta del conjunto de todas las especies en la organización de la comunidad.

9. Como consecuencia del proceso de colonización se ha producido una notable alteración del ensamblaje de las comunidades en los pastizales chilenos. El desensamblaje de las comunidades originales se hace patente por el menor nivel de segregación de las especies nativas chilenas con respecto a las especies exóticas que se han naturalizado en Chile, así como por la mayor segregación espacial de las especies colonizadoras en Chile que la observada en España.

10. Las especies nativas y exóticas juegan un rol complementario en la ontogenia de la comunidad asociada al proceso de sucesión. En una primera fase se establecen especies exóticas ruderales y asociadas a cultivos bajo las condiciones post-agrícolas, a cuya perturbación no están adaptadas las especies nativas. En una segunda fase la comunidad se compone de especies nativas y exóticas, aunque esta coexistencia se basa en dos estrategias diferentes: las exóticas son tolerantes al pastoreo mientras que las nativas se defienden de él.

11. Las especies nativas y exóticas difieren en cuanto a su carácter anual o perenne a lo largo de la sucesión. Las exóticas son eminentemente anuales, mientras que la mayoría de las perennes son nativas.

12. No hay evidencias de competencia entre especies nativas y exóticas, evitándola mediante diferentes estrategias en la ocupación del espacio. La ontogenia de la comunidad en el tiempo refleja una ganancia neta de biodiversidad, incrementándose el número de nativas y manteniéndose un pool de exóticas, lo que permite la coexistencia de ambas.

13. Hay una gran variabilidad en cuanto a los mecanismos de adaptación para las poblaciones de *Leontodon taraxacoides*, *Hypochaeris glabra* y *Trifolium glomeratum*, aunque la importancia relativa de cada mecanismo depende de la especie considerada y la variable analizada. La diferenciación ecotípica resulta importante en el caso de *T. glomeratum*, que presenta un retraso en su desarrollo fenológico conforme aumenta la precipitación de la región de origen, lo que permite a la planta disponer de más tiempo para invertir en crecimiento y producción de biomasa. La plasticidad fenotípica es el mecanismo principal de *L. taraxacoides*, lo que parece proporcionar más posibilidades adaptativas para adaptarse exitosamente a las condiciones del nuevo medio, así como una mejora en la capacidad de invasión de la especie.

14. Bajo condiciones uniformes de cultivo, las poblaciones de origen exótico y las que crecieron en las condiciones ambientales chilenas presentan mayor tasa de supervivencia que las poblaciones nativas o desarrolladas en España.

15. *L. taraxacoides* combina plasticidad fenotípica y diferenciación ecotípica, que actúan conjuntamente para aumentar la producción de semillas, así como para producir más aquenos con dispersión anemócora en las poblaciones de origen exótico. Estas co-adaptaciones a las nuevas condiciones constituyen una estrategia para incrementar la presión de propágulos, así como sus posibilidades de dispersión en el nuevo entorno, lo que maximiza su eficiencia y capacidad de colonización.

16. *L. taraxacoides* no requiere de mecanismos complejos para incrementar su capacidad de expansión: relaciones arquitectónicas relativamente simples (número y tamaño de los capítulos), que dependen en gran medida de la biomasa, así como diferentes estrategias de dispersión pueden incrementar el éxito de adaptación y de dispersión en el área invadida.

17. En contraposición a la creencia tradicional de que la naturalización de especies exóticas siempre disminuye la biodiversidad nativa o la desplaza por exclusión, la coexistencia de especies nativas y exóticas en los espinales chilenos parece pacífica, sugiriendo que procesos de facilitación pueden estar ocurriendo entre ambos tipos de especies. En este sentido, las especies exóticas parecen mejorar las duras condiciones ambientales creadas tras una perturbación, lo que permite que las especies nativas puedan re-establecerse en el territorio.

CONCLUSIONS

1. Most of Chile's non-native plants are annual species of Eurasian-Mediterranean origin. There is a relationship between regions of origin and species' biological cycle. A positive association exists between annual plants and species from the Mediterranean Basin, whereas woody plants mainly come from Africa, and America.

2. The flora of central Chile is a good expression of the country's as a whole with regard to percentages of the most represented families, life cycle and region of origin of non-native species. The most common families of the Chilean non-native flora are Poaceae, Asteraceae and Fabaceae, and the most frequent species is *Leontodon taraxacoides* (Vill.) Mérat

3. The proportion of the non-native flora in Chile tends to be greater at more detailed spatial scales, being 13% in the whole country, 18% in the central zone, and 49% in the *espinales*. The distribution of families, biogeographic origin and life cycle in the *espinales* is of the same order of magnitude as those found in Spanish *dehesas*. Both agro-silvopastoral systems are equivalent in floristic terms, although species richness is greater in Spain.

4. Climate acts as the principal predictor of species establishment potentiality at broad scale; there is a correspondence between the climatic characteristics associated with the communities in the source area and those of the recipient area. The communities related to habitats with greater anthropic influence in the source area such as ruderal and arable lands act as the main donors, although the importance of the habitat characteristics depends upon the climate in the recipient area.

5. Colonization is context- and scale-dependent; therefore its study must include territories with a wide range of environmental heterogeneity and different spatial scales. Hierarchical influence of environmental factors indicates the existence of filters that select species pre-adapted to the climatic and habitat conditions in the recipient area.

6. Environmental factors affecting species richness in the Mediterranean regions of Spain and Chile are different. In Spain, colonizer species are weakly related to a combination of soil and climate properties, whereas in Chile the number of exotic species is highly dependent on climate conditions, especially water availability.

7. Lack of relationship between native and exotic species richness indicated that biotic filters (*i.e.* species competition) are less important than abiotic ones in transcontinental naturalization in Chile.

8. The segregation of species in Spanish and Chilean communities is higher than the expected from random and species respond to the climatic and edaphic factors becoming better organized, but this pattern is expressed with different intensity in the two regions. Our results highlight inter-regional differences in the co-occurrence patterns of exclusive and colonizer species. Exclusives exhibit greater spatial segregation in Spain, whereas for colonizers it is more evident in Chile. The combination of patterns of both species groups in each country accounts for the features of all the species in the community organization.

9. As a consequence of the colonization process a noteworthy alteration of the community assembly in

Chilean grasslands has occurred. The disassembly of the original communities is shown by the lesser segregated level of the Chilean native species than the exotic species that became naturalized in Chile, and by the greater spatial segregation of colonizer species in Chile than in Spain.

10. Exotic and native species play a complementary role in the community ontogeny associated to a successional process. In a first phase, ruderal and weedy crop exotic species established under the disturbed post-agricultural conditions to which native species are not adapted. In a second phase the community is made up of native and exotic species, although based on two differentiated strategies: grazing-tolerant non-natives or grazing-defensive natives.

11. Exotic and native species differ in their life-form patterns along succession. Exotics are mainly annuals, while most perennials are natives.

12. There are no evidences of competition between exotic and native species which is due to their different strategies in the occupation of the space. Community ontogeny with time determines a net gain of biodiversity, increasing natives and maintaining a general exotic pool, allowing the coexistence of both.

13. There is great variability in adaptive mechanisms for the populations of *Leontodon taraxacoides*, *Hypochaeris glabra* and *Trifolium glomeratum*, although the relative importance of each mechanism depends on the species considered and on the variable analyzed. Ecotypic differentiation appears to be important in *T. glomeratum* which delays its phenological development when increased precipitation in the source area allowing plants to have more time to invest on growth and biomass production. Phenotypic plasticity appears to be important in *L. taraxacoides*, which seems to provide more adaptive skills to successfully adapt to changing environmental conditions, as well as to enhance the invasiveness of a species.

14. When growing in common garden conditions, exotic populations —those originated and grown in the non-native range— show greater survival rates than native ones.

15. *L. taraxacoides* combines phenotypic plasticity and ecotypic differentiation acting conjunctively to enhance seed output and produce more achenes with anemochorous dispersion in populations from exotic origin. These coadaptations to the novel conditions constitute a strategy to increase propagule pressure and spreading in the new environment in order to maximize the colonization ability and efficiency of this species.

16. *L. taraxacoides* does not require complex mechanisms to increase its capacity of expansion: simple architectural relationships (number and size of capitula), largely dependent on biomass, and different dispersal strategies can enhance the successful adaptation and spreading in its invaded range.

17. In opposition to the traditional believe that exotics' naturalization always decreases native biodiversity or displaces it by exclusion, the coexistence between native and exotic species in Chilean *espinales* appears pacific, suggesting that some benefits or facilitation processes are occurring between both types of species. Exotics seem to ameliorate the harsh environmental conditions created after a disturbance so that natives can re-establish in that area.

References

REFERENCES

Abrahamson WG, Gadgil M (1973) Growth form and reproductive effort in goldenrods (Solidago, Compositae). American Naturalist 107:651—661
Acosta-Gallo B (2005) Comportamiento de los componentes aéreo y subterráneo de pastizales en diferentes condiciones ambientales. Tesis Doctoral. Facultad de Biología, Universidad Complutense de Madrid

Acosta B, Sánchez-Jardón L, del Pozo A, García-Ibáñez E, Casado MA, Montalvo J, Pineda FD (2008) Grassland species composition and morpho-functional traits along an altitudinal gradient in a Mediterranean environment: Relationship with soil water availability and evaporative dynamic. Acta Oecologica 34:26—37

Adler PB, Milchunas DG, Lauenroth WK, Sala OE, Burke IC (2004) Functional traits of graminoids in semi-arid steppes: a test of grazing histories. Journal of Applied Ecology 41:653—663

Alexander JM, Kueffer C, Daehler CC, Edwards PJ, Pauchard A, Seipel T, MIREN Consortium (2011) Assembly of non-native floras along elevational gradients explained by directional ecological filtering. Proceedings of the National Academy of Sciences of the United States of America 108:656—661

Alexander JM, van Kleunen M, Ghezzi R, Edwards PJ (2012) Different genetic clines in response to temperature across the native and introduced ranges of a global plant invader. Journal of Ecology 100:771—781

Alpert P, Bone E, Holzapfel C (2000) Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. Perspectives in Plant Ecology, Evolution and Systematics 3:52—66

Álvarez-Pérez S, Herrera C (2013) Composition, richness and non-random assembly of culturable bacterial-microfungal communities in floral nectar of Mediterranean plants. FEMS Microbiology Ecology 83:685—699

Amir S, Cohen D (1990) Optimal reproductive efforts and the timing of reproduction of annual plants in randomly varying environments. Journal of Theoretical Biology 147:17—42

Aravena JC, Lequesne C, Jime ´nez H, Lara A, Armesto JJ (2003) Firehistory in central Chile:tree-ring evidence andmodern records. In: Veblen TT, William WL, Montenegro G, Swetnam TW (Eds.) Fire and climatic change in temperate ecosystems of the Western Americas. Springer, New York, pp 343—356

Arianoutsou M, Delipetrou P, Vilà M, Dimitrakopoulos PG, Celesti-Grapow L, Wardell-Johnson G, Henderson L, Fuentes N, Ugarte-Mendes NE, Rundel PW (2013) Comparative patterns of plant invasions in the Mediterranean Biome. PLOS ONE 8:1—13

Armas C, Pugnaire FI (2005) Plant interactions govern population dynamics in a semi-arid plant community. Journal of Ecology 93:978—989

Armas C, Schöb C, Gutiérrez JR (2013) Modulating effects of ontogeny on the outcome of plant—plant interactions along stress gradients. New phytologist 200:7—9

Armesto J, Pickett ST (1985) A mechanistic approach to the study of succession in the Chilean matorral. Revista Chilena de Historia Natural 58:9—17

Aronson J, Kigel J, Shmida A, Klein J (1992) Adaptive phenology of desert and Mediterranean populations of annual plants grown with and without water stress. Oecologia 89:17—26

Aronson J, Kigel J, Shmida, A (1993) Reproductive allocation strategies in desert and Mediterranean populations of annual plants grown with and without water stress. Oecologia 93:336—342

Aronson J, Del Pozo A, Ovalle C, Avendaño J, Lavín A, Etienne M (1998) Land use changes and conflicts in central Chile. In: Rundel PW, Montenegro G, Jaksic FM, editors. Landscape degradation and biodiversity in Mediterranean-type ecosystems. Springer-Verlag, Berlin, Germany. pp 155—168.

Arroyo MTK, Cavieres LA, Marticorena C, Muñoz-Schick M (1995a) Convergence in the Mediterranean floras in central Chile and California: insights from comparative biogeography. Ecological studies 108:43-88

Arroyo MTK, Zedler PH, Fox MD (1995b) Ecology and Biogeography of Mediterranean ecosystems in Chile, California, and Australia. Ecological studies 108. 458pp

Arroyo MTK, Cavieres L (1997) The Mediterranean type-climate flora of Central Chile. What do we know and how can we assure its protection? Noticiero de Biología (Chile) 5:48—56

Arroyo MTK, Marticorena C, Matthei O, Cavieres LA (2000) Plant invasions in Chile: present patterns and future predictions. In: Mooney HA, Hobbs RJ (Eds.) Invasive species in a changing world. Island, Washington, pp 395—421

Aschmann H (1973) Distribution and peculiarity of Mediterranean ecosystems. In: di Castri F, Mooney HA (Eds.) Mediterranean type ecosystems, origin and structure. Springer, Berlin, pp 11—19

Aschmann H, Bahre C (1977) Man's impact on the wild landscape. In: Mooney HA (Ed.) Convergent evolution of Chile and California Mediterranean climate ecosystems. Dowden, Hutchinson & Ross, Stroudsburg, pp 73—84

Aschman H (1991) Human impact on the biota of Mediterranean-climate regions of Chile and California. In: Groves RH, Di Castri F (Eds.) Biogeography of Mediterranean invasions. Cambridge University Press, Cambridge (UK)

Baer SG, Engle DM, Knops JMH, Langeland KA, Maxwell BD, Menalled FD, Symstad AJ (2009) Vulnerability of rehabilitated agricultural production systems to invasion by nontarget plant species. Environmental Management 43:189—196

Bagnouls F, Gaussen H (1953) Saison sèche et indice xérothermique. Bulletin de la Société d'Histoire Naturelle de Toulouse 88:193—240

Baier SL, Bergstrand JH (2001) The growth of world trade: tariffs, transport costs, and income similarity. Journal of International Economics 53:1—27

Baker A, O'Dowd DJ (1982) Effects of parent plant density on the production of achene types in the annual *Hypochoeris glabra*. Journal of Ecology 70:201–215

Baker HG (1965) Characteristics and modes of origin of weeds. In: Baker HG, Stebbins GL (Eds.) The genetics of colonizing species. Academic Press, New York, pp 147–169

Baker HG (1974) The evolution of weeds. Annual Review of Ecology and Systematics 5:1–24

Baker HG (1989) Some aspects of the natural history of seeds banks. In: Leck MA, Parker VT, Simpson RL (Eds.) Ecology of soil seed banks. Academic Press, San Diego, California, pp 9–21

Bannister AR, Vidal OJ, Teneb E, Sandoval V (2012) Latitudinal patterns and regionalization of plant diversity along a 4270-km gradient in continental Chile. Austral Ecology 37:500–509

Barbier EB, Knowler D, Gwatipedza J, Reichard SH, Hodges AR (2013) Implementing Policies to Control Invasive Plant Species. BioScience 63:132–138

Bartomeus I, Sol D, Pino J, Vicente P, Font X (2012) Deconstructing the native–exotic richness relationship in plants. Global Ecology and Biogeography 21:524–533

Bates D, Maechler M, Bolker B, Walker S, Christensen RHB, Singmann H (2014) lme4: Linear mixed-effects models using Eigen and S4. http://cran.r-project.org/web/packages/lme4/index.html. R package version 1.1-6

Bennett EM, Cramer W, Begossi A, Cundill G, Díaz S, Egoh BN, Geijzendorffer IR, Krug CB, Lavorel S, Lazos E, Lebel L, Martín-López B, Meyfroidt P, MooneyHA, Nel JL, Pascual U, Payet K, Harguindeguy NP, Peterson GD, Prieur-Richard AH, Reyers B, Roebeling P, Seppelt R, Solan M, Tschakert P, Tscharntke T, Turner II BL,Verburg PH, Viglizzo EF, White PCL, Woodward, G. (2015). Linking biodiversity, ecosystem services, and human well-being: three challenges for designing research for sustainability. Current Opinion in Environmental Sustainability 14:76–85

Blossey B (1999) Before, during and after: the need for long-term monitoring in invasive pplant species management. Biological Invasions 1:301–311

Boessneck J, von den Driesch A (1980) Finds of animal bones from four caves in southern Spain (original in German). In: Boessneck J, von den Driesch A (Eds.) Studies on finds of early animal bones from the Iberian Peninsula 7. Institut für Palaeoanatomir, Domestikationsforschung und Geschichte de Tiermedizin der Universität München, Munich, pp1–83

Bradley NL, Leopold AC, Ross J, Huffaker W (1999) Phenological changes reflect climate change in Wisconsin. Proceedings of the National Academy of Sciences of the United States of America 96:9701–9704

Bradley BA, Blumenthal DM, Early R, Grosholz ED, Lawler JJ, Miller LP, Sorte CJB, D'Antonio CM, Diez JM, Dukes JS, Ibañez I, Olden JD (2012) Global change, global trade, and the next wave of plant invasions. Frontiers in Ecology and the Environment 10:20–28

Bradshaw WE, Holzapfel CM (2008) Genetic response to rapid climate change: it's seasonal timing that matters. Molecular Ecology 17:157–166

Brändel M (2007) Ecology of achene dimorphism in *Leontodon saxatilis*. Annals of Botany 100:1189–1197

Brock JH, Wade M, Pyšek P, Green D (1997) Plant Invasions: Studies from North America and Europe. Backhuys, Leiden

Brown TA, Jones AK, Powell W, Allaby RG (2008) The complex origins of domesticated crops in the Fertile Crescent. Trends in Ecology and Evolution 24:103–109

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: A practical information-theoretic approach (2nd edition). Springer-Verlag, New York

Buswell JM, Moles AT, Hartley S (2011) Is rapid evolution common in introduced plant species? Journal of Ecology 99:214–224

Calcagno V, de Mazancourt C (2010) glmulti: an R package for easy automated model selection with (generalized) linear models. J Stat Soft 34:1–29

Caley P, Groves RH, Barker R (2008) Estimating the invasion success of introduced plants. Diversity and Distributions 14:196–203

Callaway RM, Aschehoug ET (2000) Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. Science 290:521–523

Callaway RM, Ridenour WM (2004) Novel weapons: invasive success and the evolution of increased competitive ability. Frontiers in Ecology and Environment 2:436–443

Cardinale BJ, Duffy JE, Gonzalez A, Hooper DU, Perrings C, Venail P, Narwani A, Mace GM, Tilman D, Wardle DA, Kinzig AP, Daily GC, Loreau M, Grace JB, Larigauderie A, Srivastava DS, Naeem S (2012) Biodiversity loss and its impact on humanity. Nature 486:59–67

Carey MP, Sanderson BL, Barnas KA, Olden JD (2012) Native invaders-challenges for science, management, policy, and society. Frontiers in Ecology and the Environment 10:373–381

Cariola C, Sunkel O (1982) Un siglo de historia económica de Chile 1830–1930, dos ensayos y una bibliografía. Ediciones cultura hispánica del Instituto de Cooperación Iberoamericana. Madrid (España)

Carpenter S, Mooney HA, Agard J, Capistrano D, DeFries RS, Díaz S, Dietz T, Duraiappah AK, Oteng-Yeboah A, Pereira EM, Perrings C, Rield WV, Sarukhan J, Schies RJ, Whyte A (2009) Science for managing ecosystem services: Beyond the millennium assessment. Proceedings of the National Academy of Science of the United States if America 106: 1305–1312

Casado MA, de Miguel JM, Sterling A, Peco B, Galiano EF, Pineda FD (1986) Production and spatial structure of Mediterranean pastures in different stages of ecological succession. Vegetatio 64:75–86

Casado MA, Acosta-Gallo B, Sánchez-Jardón L, Martín-Forés I, Castro I, Ovalle C, del Pozo A, de Miguel JM (2015) Interactive effects of source and recipient habitats on plant invasions: distribution of exotic species in Chile. Diversity and Distributions 21:609–619

Castroviejo S, coord. (1986-2014) Flora Ibérica, vols. 1-8, 10-15, 17-18, 20-21. Real Jardín Botánico de Madrid, C.S.I.C. Madrid

Castro SA, Figueroa JA, Muñoz-Schick M, Jaksic FM (2005) Minimum residence time, biogeographical origin, and life cycle as determinants of the geographical extent of naturalized plants in continental Chile. Diversity and Distributions 11:183–191

Castro SA, Jaksic FM (2008) How general are global trends in biotic homogenization? Floristic tracking in Chile, South America. Global Ecology and Biogeography 17:524–531

Catford JA, Jansson R, Nilsson C (2009) Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. Diversity and Distributions 15:22–40

CBD (2014) Global Biodiversity Outlook 4. Secretariat of the Convention on Biological Diversity, Montreal

Chambel MR, Climent J, Alía R, Valladares F (2005) Phenotypic plasticity: a useful framework for understanding adaptation in forest species. Investigación Agraria. Sistema y recursos forestales 14:334–344

Chase JM (2003) Community assembly: when should history matter? Oecologia 136:489–498

Chiarucci A (2007) To sample or not to sample? That is the question...for the vegetation scientist. Folia Geobotanica 42:209–216

Chytrý M, Otypková Z (2003) Plot sizes used for phytosociological sampling of European vegetation. Journal of Vegetation Science 14:563–570

Chytrý M, Maskell LC, Pino J, Pyšek P, Vilà M, Font X, Smart SM (2008) Habitat invasions by alien plants: a quantitative comparison among Mediterranean, subcontinental and oceanic regions of Europe. Journal of Applied Ecology 45:448–458

Chytrý M, Pyšek P, Wild J, Pino J, Maskell L, Vilà M (2009) European map of alien plant invasions based on the quantitative assessment across habitats. Diversity and Distributions 15:98–107

Chytrý M, Schaminée JH, Schwabe A (2011) Vegetation survey: a new focus for applied vegetation science. Applied Vegetation Science 14:435–439

Cleland EE, Smith MD, Andelman SJ, Bowles C, Carney KM, Horner-Devine MC, Drake JM, Emery SM, Gramling JM, Vandermast DB (2004) Invasion in space and time: nonnative species richness and relative abundance respond to interannual variation in productivity and diversity. Ecology Letters 7:947–957

Cocks PS, Craig AD, Kenyon RV (1982) Evolution of subterranean clover in South Australia. II. Change in genetic composition of a mixed population after 19 years' on a commercial farm. Australian Journal of Agrarian Research 33:679–695

Cohen D, Levin SA (1991) Dispersal in patchy environments: the effects of temporal and spatial structure. Theoretical Population Biology 39:63–99

Colautti RI, MacIsaac HJ (2004) A neutral terminology to define 'invasive'species. Diversity and Distributions 10:135-141

Compagnoni A, Halpern CB. Properties of native plant communities do not determine exotic success during early forest succession. Ecography 2009; 32:449–458

Connor EF, Simberloff D (1979) The assembly of species communities: chance or competition? Ecology 60:1132–1140

Corbin JD, D'Antonio CM (2004) Competition between native perennial and exotic annual grasses: implications for an historical invasion. Ecology 85:1273–1283

Core Team R (2013) R: A language and environment for statistical computing. R Found Stat Comput, Vienna

Cornwell WK, Ackerly DD (2009) Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. Ecological Monographs 79:109–126

Corvalan C, Hales S, McMichael A (2005) Ecosystems and human well-being: health synthesis, a report for the Millennium Ecosystem Assessment. World Health Organization, Geneva

Courchamp F, Caut S, Bonnaud E, Bourgeois K, Angulo E, Watari Y (2011) Eradication of alien invasive species: surprise effects and conservation successes. In: Veitch CR, Clout MN, Towns DR (Eds.) Island invasives: eradication and management, pp. 285-289. IUCN, Gland, Switzerland

Cowling RM, Campbell BM (1980) Convergence in vegetation structure in the Mediterranean communities of California, Chile and South Africa. Vegetatio 43:191–197

Cowling RM, Rundel PW, Lamont BB, Arroyo MK, Arianoutsou M (1996) Plant diversity in Mediterranean climate regions. Trends in Ecology and Evolution 11:362–366

Cox GW (2004) Alien species and evolution. Island Press, Washington, 344 pp

Cramer VA, Hobbs RJ, Standish RJ (2008) What's new about old fields? Land abandonment and ecosystem assembly. Trends in Ecology and Evolution 23:104–112

Cronk QCB, Fuller JL (1995) Plant invaders: The threat to natural ecosystems. Chapman and Hall, London, 256pp

Crutzen PJ (2002) Geology of mankind. Nature 415:23–23

D'Antonio CM (2000) Fire, plant invasions, and global changes. In: Mooney H, Hobbs RJ. Invasive species in a changing world, 63-95. Eds. Island Press. Washington, D.C (USA)

D'Antonio CM, Mahall BE (1991) Root profiles and competition between the invasive, perennial, *Carpobrotus edulis*, and two native shrub species in California coastal scrub. American Journal of Botany 78:885–894

D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass fire cycle, and global change. Annual Review of Ecology and Systematics 23:63–87

Dainese M, Poldini L (2012) Does residence time affect responses of alien species richness to environmental and spatial processes? NeoBiota 14:47–66

Davidson AM, Jennions M, Nicotra AB (2011) Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. Ecology Letters 14:419—431

Davis H (1894) California breadstuffs. The Journal of Political Economy 2:517—535

Davis MA (2003) Biotic globalization: does competition from introduced species threaten biodiversity? Bioscience 53:481—489

Davis MA, Grime J, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology 88:528—534

Davis MA, Chew MK, Hobbs RJ, Lugo AE, Ewel JJ, Vermeij GJ, Brown JH, Rosenzweig ML, Gardener MR, Carroll SP, Thompson K, Pickett STA, Stromberg JC, Del Tredici P, Suding KN, Ehrenfeld JG, Grime JP, Mascaro J, Briggs JC (2011) Don't judge species on their origins. Nature 474:153—154

Dawson W, Burslem DF & Hulme PE (2009) Factors explaining alien plant invasion success in a tropical ecosystem differ at each stage of invasion. Journal of Ecology 97:657—665

De'ath G, Fabricius KE (2000) Classification and regression trees: a powerful yet simple technique for ecological data analysis. Ecology 81:3178—3192

de Bello F, Lepš J, Sebastia MT (2005) Predictive value of plant traits to grazing along a climatic gradient in the Mediterranean. Journal of Applied Ecology 42:824—833

De Miguel JM, Casado MA, Del Pozo A, Ovalle C, Moreno-Casasola P, Travieso-Bello AC, Barrera M, Ricardo N, Tecco PA, Acosta B (2010) How reproductive, vegetative and defensive strategies of Mediterranean grassland species respond to a grazing intensity gradient. Plant Ecology 210:97—110

De Miguel JM, Acosta B, Gómez Sal A (2013) Understanding Mediterranean pasture dynamics: general tree cover vs. specific effects of individual trees. Rangeland Ecology and Management 66:216—223

del Pozo A, Ovalle C, Aronson J, Avendaño J (2000) Developmental responses to temperature and photoperiod in ecotypes of *Medicago polymorpha* L. along an environmental gradient in central Chile. Annals of Botany 85:809—814

del Pozo A, Ovalle C, Aronson J, Avendaño J (2002a) Ecotypic differentiation in *Medicago polymorpha* L. along an environmental gradient in central Chile. I. Phenology, biomass production and reproductive patterns. Plant Ecology 159:119—130

del Pozo A, Ovalle C, Aronson J, Avendaño J (2002b) Ecotypic differentiation in *Medicago polymorpha* L. along an environmental gradient in central Chile. II. Winter growth as related to phenology and temperature regime. Plant Ecology 160:53—59

del Pozo A, Ovalle C, Casado MA, Acosta B, De Miguel JM (2006) Effects of grazing intensity in grasslands of the *Espinal* of central Chile. Journal of Vegetation Science 17:791—798

Di Castri F (1968) Esquisse écologique du Chili. In: Biologie de l'Amérique australe. Tome IV, 7—52. C.N.R.S. Paris (France)

Di Castri F (1981) Mediterranean-type shrublands of the world. In: Di Castri F, Goodall DW, Specht RL (Eds.) Mediterranean-type shrublands, 1—52. Elsevier. Amsterdam (Netherlands)

Di Castri F (1989) History of biological invasions with special emphasis on the Old World. In: Drake JA, Mooney HA, di Castri F, Groves RH, Kruger FJ, Rejmánek M, Williamson M (Eds.) Biological invasions: a global perspective, pp. 1—30. John Wiley and Sons, Chichester, UK

Di Castri F (1991) An ecological overview of the five regions of the world with Mediterranean climate. In: Groves H, Di Castri F (Eds.) Biogeography of Mediterranean invasions, Cambridge University Press. Cambridge (UK)

Di Castri F, Goodall DW, Specht RL (1981) Mediterranean type Shrublands. UNESCO, Elsevier

Diamond JM (1975) Assembly of species communities. In: Cody ML, Diamond J (Eds.) Ecology and evolution of communities. Harvard University Press, Cambridge, Massachusetts, pp. 342—444.

Díaz S, Fargione J, Chapin FS III, Tilman D (2006) Biodiversity Loss Threatens Human Well-Being. PLoS Biology 4:e277

Díaz S, Lavorel S, Mcintyre S, Falczuk V, Casanoves F, Milchunas DG, Skarpe C, Rusch G, Sternberg M, Noy-Meir I, Landsberg J, Zhang W, Clark H, Camprbell BD (2007) Plant trait responses to grazing – a global synthesis. Global Change Biology 13:313—341

Díaz S, Demissew S, Carabias J, Joly C, Lonsdale M, Ash N, et al. (2015) The IPBES Conceptual Framework—connecting nature and people. Current Opinion in Environmental Sustainability 14:1—16

DiTomaso JM, Healy EA (2007) Weeds of California and other western states. Vol. 3488. UCANR Publications. Oakland, CA

Dlugosch KM, Parker IM (2008) Founding events in species invasions: genetic variation, adaptive evolution, and the role of multiple introductions. Molecular Ecology 17:431—449

Donoso C, Lara A (1996) Utilización de los bosques nativos en Chile: pasado, presente y futuro. In: Armesto JJ, Villagran C, Arroyo MK (Eds.) Ecología de los bosques nativos de Chile, 363—387. Editorial Universitaria. Santiago (Chile)

Donoso C (1993) Bosques templados de Chile y Argentina: variación, estructura y dinámica. Universitaria. Santiago (Chile)

Dostál P (2011) Plant competitive interactions and invasiveness: searching for the effects of phylogenetic relatedness and origin on competition intensity. The American Naturalist 177:655—667

Dostál P, Weiser M, Koubek T (2012) Native jewelweed, but not other native species, displays post-invasion trait divergence. Oikos 121:1849—1859

Dostál P, Dawson OW, van Kleunen M, Keser LH, Fischer M (2013) Central European plant species from more productive habitats are more invasive at a global scale. Global Ecology and Biogeography 22:64—72

Dukes JS, Mooney HA (1999) Does global change increase the success of biological invaders? Trends in Ecology and Evolution 14:135—139

Dukes JS, Mooney HA (2004) Disruption of ecosystem processes in western North America by invasive species. Revista Chilena de Historia Natural

77:411—437

Dümenil-Gates L, Liess S (2001) Impacts of deforestation and afforestation in the Mediterranean region as simulated by the MPI atmospheric GCM. Global and Planetary Change 30:309—328

Echeverría C, Coomes D, Salas J, Rey-Benayas JM, Lara A, Newton A (2006) Rapid deforestation and fragmentation of Chilean Temperate Forests. Biological Conservation 130:451—494

Ehrman T, Cocks PS (1990) Ecogeography of annual legumes in Syria: distribution patterns. Journal of Applied Ecology 27:578—591

Ehrman T, Cocks PS (1996) Reproductive patterns in annual legume species on an aridity gradient. Vegetatio 122:47—59

Elton CS (1958) The Ecology of invasions by animals and plants. Methuen, London

Essl F, Dullinger S, Rabitsch W, Hulme PE, Wilson JRU, Richardson DM (2015) Delayed biodiversity change: no time to waste. Trends in Ecology and Evolution (in press) doi: 10.1016/j.tree.2015.05.002

Estévez J (1988) Study of the faunal remains (original in Spanish). Cova Fosca, ed Olaria C (Servico de Publicaciones Diputación de Castellón, Castellón, Spain), pp 281—337

Figueroa JA, Castro SA, Marquet PA, Jaksic FM (2004) Exotic plant invasions to the Mediterranean region of Chile: causes, history and impacts. Revista Chilena de Historia Natural 77:465—483

Figueroa JA, Teillier S, Castro SA (2011) Diversity patterns and composition of native and exotic floras in central Chile. Acta Oecologica 37:103—109

Figueroa ME, Davy JA (1991) Response of Mediterranean grassland species to changing rainfall. Journal of Ecology 79:925—941

Fine PVA, Kembel SW (2011) Phylogenetic community structure and phylogenetic turnover across space and edaphic gradients in western Amazonian tree communities. Ecography 34:552—565

Flint SD, Palmblad IG (1978) Germination dimorphism and developmental flexibility in the ruderal weed *Heterotheca grandiflora*. Oecologia 36:33—43

Fogarty G, Facelli JM (1999) Growth and competition of *Cytisus scoparius*, an invasive shrub, and Australian native shrubs. Plant Ecology 144:27—35

Follmann G, Matte V (1963) Estepas sin jirafas. Universidad de Chile, Santiago, Chile. Boletín Técnico 42:45—48

Font Tullot I (2000) Climatología de España y Portugal. Ediciones Universidad de Salamanca, Salamanca

Fox GA (1989) Consequences of flowering-time variation in a desert annual: Adaptation and history. Ecology 70:1294—1306

Fox GA (1990) Drought and the evolution of flowering time in desert annuals. American Journal of Botany 77:1508—1518

Fox MD (1990) Mediterranean weeds: exchanges of invasive plants between the five Mediterranean regions of the world. In: Di Castri F, Hansen AJ, Debussche M (Eds.) Biological invasions in Europe and the Mediterranean basin, pp. 179—200. Springer Netherlands

Funk JL (2008) Differences in plasticity between invasive and native plants from a low resource environment. Journal of Ecology 96:1162—1173

Funk JL, Vitousek PM (2007) Resource-use efficiency and plant invasion in low-resource systems. Nature 446:1079—1081

Fuentes N, Ugarte E, Kühn I, Klotz S (2008) Alien plants in Chile: inferring invasion periods from herbarium records. Biological Invasions 10:649—657

Fuentes N, Pauchard A, Sánchez P, Esquivel J, Marticorena A (2013) A new comprehensive database of alien plant species in Chile based on herbarium records. Biological Invasions 15:847—858

Fuenzalida H, Pisano E (1965) Biografía. In: Corfo (Ed.) Geografía Económica de Chile, 228-267. Santiago (Chile)

Gaertner M, Breeyen AD, Hui C, Richardson M (2009) Impacts of alien plant invasions on species richness in Mediterranean-type ecosystems: a meta-analysis. Progress in Physical Geography 33:319—338

Galen C, Shore JS, Deyoe H (1991) Ecotypic divergence in alpine Polemonium viscosum: genetic structure, quantitative variation and local adaptation. Evolution 45:1218—1228

García-Llorente M, Martín-López B, González JA, Alcorlo P, Montes C (2008) Social perceptions of the impacts and benefits of invasive alien species: Implications for management. Biological Conservation 141:2969-2983

García-Llorente M, Martín-López B, Nunes PA, González JA, Alcorlo P, Montes C (2011) Analyzing the social factors that influence willingness to pay for invasive alien species management under two different strategies: eradication and prevention. Environmental management 48:418-435

Gaston KJ, Jones AG, Hänel C, Chown SL (2003) Rates of species introduction to a remote oceanic island. Proceedings of the Royal Society of London B 270:1091—1098

Gay C (1845—1854) Historia física y política de Chile. Botánica (Flora chilena). 8 Volume, 1 Atlas. Santiago (Chile) and Paris (France)

Gea-Izquierdo G, Allen-Diaz B, Miguel AS, Canellas I (2010) How do trees affect spatio-temporal heterogeneity of nutrient cycling in Mediterranean annual grassland? Annals of Forest Science 67:112

Geng YP, Pan XY, Xu CY, Zhang WJ, Li B, Chen JK, Lu BR, Song ZP (2007) Phenotypic plasticity rather than locally adapted ecotypes allows the invasive alligator weed to colonize a wide range of habitats. Biological Invasions 9:245—256

Gilbert B, Lechowicz MJ (2005) Invasibility and abiotic gradients: the positive correlation between native and exotic plant diversity. Ecology 86:1848—1855

Gómez-González S, Cavieres LA (2009) Litter burning does not equally affect seedling emergence of native and alien species of the Mediterranean-type Chilean matorral. International Journal of Wildland Fire 18:213—221

Gómez-González S, Torres-Díaz C, Valencia G, Torres-Morales P, Cavieres LA, Pausas JG (2010) Anthropogenic fires increase alien and native annual species in the Chilean coastal matorral. Diversity and Distributions 17:58—67

González-Moreno P, Diez JM, Ibáñez I, Font X, Vilà M (2014) Plant invasions are context-dependent: multiscale effects of climate, human activity and habitat. Diversity and Distributions 20:720—731

Gotelli NJ (2000) Null model analysis of species co-occurrence patterns. Ecology 81:2606—2621

Gotelli NJ, Entsminger GL (2012) EcoSim: Null Models Software for Ecology, v. 7.0. <http:// garyentsminger.com/ecosim/index.htm>

Gotelli NJ, Graves GR (1996) Null models in ecology. Smithsonian Institution Press Washington, DC

Gotelli NJ, McCabe DJ (2002) Species co-occurrence: a meta-analysis of J.M. Diamond's assembly rules model. Ecology 83:2091—2096

Götzenberger L, de Bello F, Bråthen KA, Davison J, Dubuis A, Guisan A, Lepš J, Lindborg R, Moora M, Pärtel M, Pellissier L, Pottier J, Vittoz P, Zobel K, Zobel M (2011) Ecological assembly rules in plant communities—approaches, patterns and prospects. Biological Reviews 87:111—127

Graff P, Aguiar MR, Chaneton EJ (2007) Shifts in positive and negative plant interactions along a grazing intensity gradient. Ecology 88:188—199

Gratani L (2014) Plant Phenotypic Plasticity in Response to Environmental Factors. Advances in Botany, 17pp. http://dx.doi.org/10.1155/2014/208747

Grenon M, Batisse M (1989) Futures for the Mediterranean: the blue plan. Oxford University Press, Oxford (UK)

Greuter W (1994) Extinction in Mediterranean areas. Philosophical Transactions of the Royal Society, Series B, Biological Sciences 344:41—46

Grime JP (1979) Plant Strategies and Vegetation Processes. Wiley, Chichester

Groves RH (1986) Invasion of Mediterranean ecosystems by weeds. In: Dell B, Hopkins AJM, Lamont BB (Eds.) Resilience in Mediterranean-type ecosystems. Dr. W. Junk Publishers, Dordrecht, The Netherlands, pp. 129—145

Groves RH, Burdon JJ (1986) Ecology of biological invasions: An Australian perspective. Australian Academy of Science, Canberra

Groves RH, Di Castri F (Eds.) (1991) Biogeography of Mediterranean Invasions. Cambridge University Press, Cambridge (UK), 485 pp

Groves RH, Hosking JR, Batianoff GN, Cooke DA, Cowie ID, Johnson RW, Keighery GJ,Lepschi BJ, Mitchell AA, Moerkerk M, Randall RP, Rozefelds AC, Walsh NG, Waterhouse BM (2003) Weed categories for natural and agricultural ecosystem management. Canberra, Australia: Bureau of Rural Sciences

Guerin G, Martín-Forés I, Biffin E, Baruch Z, Breed MF, Christmas MJ, Cross HB, Lowe AJ (2014) Global change community ecology beyond species-sorting: a quantitative framework based on Mediterranean-biome examples. Global Ecology and Biogeography 23:1062—1072

Gulmon SL (1977) A comparative study of the grasslands of California and Chile. Flora 66:261—278

Guo QF, Qian H, Ricklefs RE, Xi WM (2006) Distribution of exotic plants in eastern Asia and North America. Ecology Letters 9:827—834

Gurevitch J, Fox GA, Wardle GM, Inderjit, Taub D (2011) Emergent insights from the synthesis of conceptual frameworks for biological invasions. Ecology Letters 14:407—418

Gutiérrez JL, Jones CG, Sousa R (2014) Toward an integrated ecosystem perspective of invasive species impacts. Acta Oecologica 54:131—138

Hall CM (2015) Tourism and biological exchange and invasions: a missing dimension in sustainable tourism? Tourism Recreation Research 40:81—94

Hamilton MA, Murray BR, Cadotte MW, Hose GC, Baker AC, Harris CJ, Licari D (2005) Life-history correlates of plant invasiveness at regional and continental scales. Ecology Letters 8:1066—1074

Haider S, Alexander JM, Dietz H, Trepl L, Edwards PJ, Kueffer C (2010) The role of bioclimatic origin, residence time and habitat context in shaping non-native plant distributions along an altitudinal gradient. Biological Invasions 12:4003—4018

Harrison S, Grace JB (2007) Biogeographic affinity helps explain productivity-richness relationships at regional and local scales. American Naturalist 170:S5—S15

Harper JL (1977) Population Biology of Plants. Academic Press, London.

Hayes GF, Holl KD (2003) Cattle grazing impacts on annual forbs and vegetation composition of mesic grasslands in California. Conservation Biology 17:1694—1702

Heger T, Trepl L (2013) Predicting biological invasions. Biological Invasions 5:313—321

Hejda M, Pyšek P, Jarošík V (2009a) Impact of invasive plants on the species richness, diversity and composition of invaded communities. Journal of Ecology 97:393—403

Hejda M, Pyšek P, Pergl J, Sádlo J, Chytrý M, Jarošík V (2009b) Invasion success of alien plants: do habitat affinities in the native distribution range matter? Global Ecology and Biogeography 18:372—382

Hierro JL, Maron JL, Callaway RM (2005) A biogeographical approach to plant invasions: the importance of studying exotics in their introduced and native range. Journal of Ecology 93:5—15

Higgins SI, Richardson DM, Cowling RM, Trinder-Smith TH (1999) Predicting the landscape scale distribution of alien plants and their threat to plant diversity. Conservation Biology 13:303—313

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25:1965—1978

Hillebrand H, Matthiessen B (2009) Biodiversity in a complex world: consolidation and progress in functional biodiversity research. Ecology Letters 12:1405—1419

Hillerislambers J, Yelenik SG, Colman BP, Levine JM (2010) California annual grass invaders: the drivers or passengers of change? Journal of Ecology 98:1147–1156

HilleRisLambers J, Adler PB, Harpole WS, Levine JM, Mayfield MM (2012) Rethinking community assembly through the lens of coexistence theory. Annual Review of Ecology, Evolution, and Systematics 43:227–248

Hobbs RJ (1998) Impacts of land use on biodiversity in south western Australia. In: Rundel PW, Montenegro G, Jaksic FM (Eds.) Landscape disturbance and biodiversity in Mediterranean-type ecosystems. Springer-verlag. Berlin (Germany)

Holmgren M (2002) Exotic herbivores as drivers of plant invasions and switch to ecosystem alternative states. Biological Invasions 4:25–33

Holmgren M, Aviles R, Sierralta L, Segura AM, Fuentes ER (2000) Why have European herbs so successfully invaded the Chilean matorral? Effects of herbivory, soil nutrients, and fire. Journal of Arid Environment 44:197–211

Holmgren M, Aviles R, Sierralta L, Segura AM, Fuentes ER (2000) Why have European herbs so successfully invaded the Chilean matorral? Effects of herbivory, soil nutrients, and fire. Journal of Arid Environment 44:197–211

Hooper DU, Adair EC, Cardinale BJ, Byrnes JEK, Hungate BA, Matulich KL, Gonzalez A, Duffy JE, Gamfeldt L, O'Connor MI (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature 486:105–109

Houlahan JE, Findlay CS (2004) Effect of invasive plant species on temperate wetland plan diversity. Conservation Biology 18:1132–1138

Hui C, Richardson DM, Pyšek P, Le Roux JJ, Kučera T, Jarošík V (2013) Increasing functional modularity with residence time in co-distribution of native and introduced vascular plants. Nature Communications 4:245

Hulme PE (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. Journal of Applied Ecology 46:10–18

Hulme PE (2015) Invasion pathways at a crossroad: policy and research challenges for managing alien species introductions. Journal of applied ecology (in press) doi: 10.1111/1365-2664.12470

Humphries SE, Groves RH, Mitchell DS (1991) Plant invasions of Australian ecosystems: A status review and management directions. Kowari 2:1–134

Huston MA (1994) Biological diversity: the coexistence of species on changing landscapes. Cambridge University Press, Cambridge

IBM Corp. Released 2013. IBM SPSS Statistics for Windows, Version 22.0. Armonk, NY: IBM Corp

Imbert E (1999) The effects of achene dimorphism on the dispersal in time and space in *Crepis sancta* (Asteraceae). Canadian Journal of Botany 77:508–513

Imbert E (2001) Capitulum characters in the seed heteromorphic species *Crepis sancta* (Asteraceae), variance portioning and inference for the evolution of dispersal rate. Heredity 86:78–86

Imbert E (2002) Ecological consequences and ontogeny of seed heteromorphism. Perspectives in Plant Ecology, Evolution and Systematics 5:13-36

Imbert E, Escarré J, Lepart J (1996) Achene dimorphism and among-population variations in some biological traits in *Crepis sancta* (Asteraceae). International Journal of Plant Sciences 157:309–315

Imbert E, Escarré J, Lepart J (1997) Seed heteromorphism in *Crepis sancta* (Asteraceae), performance of two morphs in different environments. Oikos 79:325–332

INE (2002) Enfoque estadístico. Nuevas regiones de Chile. Boletín Informativo del Instituto Nacional de Estadística, 10 de octubre de 2007 (www.ine.cl/canales/sala_prensa/noticias/2007/octubre/files/INENuevasRegiones.pdf)

IPCC (2014) Climate Change 2014. Synthesis Report

Jaksic FM, Soriger RC (1981) Predation upon the European rabbit *(Oryctolagus cuniculus)* in Mediterranean habitats of Chile and Spain: a comparative analysis. Journal of Animal Ecology 50:269281

Jaksic FM (1998) Vertebrate invaders and their ecological impacts in Chile. Biodiversity Conservation 7:1427–1445

Jansen F, Ewald J, Zerbe S (2011) Ecological preferences of alien plant species in North-Eastern Germany. Biological Invasions 13:2691–2701

Jauni M, Gripenberg S, Ramula S (2015) Non-native plant species benefit from disturbance: a meta-analysis. Oikos 124:122–129

Jeffers ES, Bonsall MB, Froyd CA, Brooks SJ, Willis KJ (2015) The relative importance of biotic and abiotic processes for structuring plant communities through time. Journal of Ecology 103:459–472

Johnstone IM (1986) Plant invasion windows: a time-based classification of invasion potential. Biological Reviews 61:369–394

Jiménez A, Pauchard A, Cavieres LA, Marticorena A, Bustamante RO (2008) Do climatically similar regions contain similar alien floras? A comparison between the Mediterranean areas of central Chile and California. Journal of Biogeography 35:614–624

Jiménez MA, Jaksic FM, Armesto JJ, Gaxiola A, Meserve PL, Kelt DA, Gutiérrez JR (2011) Extreme climatic events change the dynamics and invisibility of semi-arid annual plant communities. Ecology Letters 14:1227–1235

Joffre R, Rambal S, Ratte P (1999) The *dehesa* system of southern Spain and Portugal as a natural ecosystem mimic. Agroforestry Systems 45:57–79

Kalusová V, Chytrý M, Kartsez JT, Nisihino M, Pyšek P (2013) Where do they come from and where they go? European natural habitats as donors of invasive alien plants globally. Diversity and Distributions 19:199–214

Kalusová V, Chytrý M, Peet RK, Wentworth TR (2014) Alien species pool influences the level of habitat invasion in intercontinental exchange of alien plants. Global Ecology and Biogeography 23:1366–1375

Keddy P, Weiher E (1999) Introduction: The scope and goals of research on assembly rules. In: Weiher W, Keddy P (eds) Ecological assembly rules, per-

spectives, advances, retreats, pp 1–20. Cambridge Univ. Press, Cambridge, UK.

Keeley SC, Johnson AW (1977) A comparison of the pattern of herb and shrub growth in comparable sites in Chile and California. The American Midland Naturalist 97:120–132

Kennedy TA, Naeem S, Howe KM, Knops JMH, Tilman D, Reich P (2002) Biodiversity as a barrier to ecological invasion. Nature 417:636–638

Kigel J (1992) Diaspore heteromorphism and germination in populations of the ephemeral *Hedypnois rhagadioloides* (L.) F.W. Schmidt (Asteraceae) inhabiting a geographic range of increasing aridity. Acta Oecologica 13:45–53

Kimball S, Schiffman PM (2003) Differing effects of cattle grazing on native and alien plants. Conservation Biology 17:1681–1693

Kleyer M, Dray S, de Bello F, Lepš J, Pakeman RJ, Strauss B, Thuiller W, Lavorel S (2012) Assessing species and community functional responses to environmental gradients: which multivariate methods? Journal of Vegetation Science 23:805–821

Kloot PM (1991) Invasive plants of the southern Australia. In: Groves RH, Di Castri F (Eds.) Biogeography of Mediterranean invasions, 131–143. Cambridge University Press. Cambridge (UK)

Kolar CS, Lodge DM (2001) Progress in invasion biology predicting invaders. Trends in Ecology and Evolution 16:199–204

Kreyling J, Beierkuhnlein C, Ellis L, Jentsch A (2008) Invasibility of grassland and heath communities exposed to extreme weather events—additive effects of diversity resistance and fluctuating physical environment. Oikos 117:1542–1554

Kruger FJ, Breytenbach GJ, Macdonald IAW, Richardson DM (1989) The characteristics of invaded Mediterranean-climate regions. In: Drake JA, Mooney, HA, Di Castri F, Groves RH, Kruger FJ, Rejmánek M, Williamson M (Eds.) Biological invasions: a global perspective. John Wiley & Sons. New York, USA

Kueffer C, Daehler CC, Torres-Santana CW, Lavergne C, Meyer JY, Otto R, Silva L. (2010) A global comparison of plant invasions on oceanic islands. Perspectives in Plant Ecology, Evolution and Systematics 12:145–162

Kulmatiski A (2006) Exotic plants establish persistent communities. Plant Ecology 187:261–275

Kumschick S, Hufbauer RA, Alba C, Blumenthal DM (2013) Evolution of fast-growing and more resistant phenotypes in introduced common mullein *(Verbascum thapsus)*. Journal of Ecology 101:378–387

Lambdon P, Lloret F, Hulme P. (2008) Do alien plants on Mediterranean islands tend to invade different niches from native species? Biological Invasions 10:703–716.

Lankau RA, Nuzzo V, Spyreas G, & Davis AS (2009) Evolutionary limits ameliorate the negative impact of an invasive plant. Proceedings of the National Academy of Sciences of the United States of America 106:15362–15367

Le Floc'h E (1991) Invasive plants of the Mediterranean Basin. In: Groves RH, Di Castri F. Biogeography of Mediterranean invasions, 67-80. Eds. Cambridge University Press. Cambridge (UK)

Le Houérou HN (1981) Impact of man and his animals on Mediterranean vegetation. In: Di Castri F, Goodall DW, Specht RL (Eds.) Mediterraneantype shrublands. Elsevier. Amsterdam (The Netherlands)

Le Houérou NH (1991) Plant invasion in the rangelands of the isoclimatic Mediterranean zone. In: Groves RH, Di Castri F (Eds.) Biogeography of Mediterranean invasions. Cambridge University Press, Cambridge, pp. 393-404

Lee WG, Tanentzap AJ, Heenan PB (2012) Plant radiation history affects community assembly: evidence from the New Zealand alpine. Biology Letters 8:558–561

Leishman MR, Cooke J, Richardson DM (2014) Evidence for shifts to faster growth strategies in the new ranges of invasive alien plants. Journal of Ecology 102:1451–1461

Leiva MJ, Chapin FS, III, Fernández Ales R (1997) Differences in species composition and diversity among Mediterranean grasslans with differente history. The case of California and Spain. Ecography 20: 97–106

Lev-Yadun S, Gopher A, Abbo S (2000) The cradle of agriculture. Science 288:1602-1603

Levine JM, D'Antonio CM (1999) Elton revisited: a review of evidence linking diversity and invisibility. Oikos 87:15–26

Levine JM, D'Antonio CM (2003) Forecasting biological invasions with increasing international trade. Conservation Biology 17:322–326

Levine JM, Vilà M, D'Antonio CM, Dukes JS, Grigulis K, Lavorel S (2003) Mechanisms underlying the impacts of exotic plant invasions. Proceedings of the Royal Society B: Biological Sciences 270:775–781

Lilley PL, Mark Vellend M (2009) Negative native exotic diversity relationship in oak savannas explained by human influence and climate. Oikos 118:1373–1382

Lionello P, Malanotte-Rizzoli P, Boscolo R, Alpert P, Artale V, Li L Luterbacher J, May W, Trigo R, Tsimplis M, Ulbrich U, Xoplaki E (2012) The Mediterranean Climate: An Overview of the Main Characteristics and Issues. Developments in Earth and environmental sciences 4:1–26

Lloret F, Medail F, Brundu G, Camarda I, Moragues E, Rita J, Lambdon B, Hulme P (2005) Species attributes and invasion success by alien plants in Mediterranean islands. Journal of Ecology 93:512–520

Lockwood JL, Cassey P, Blackburn T (2005) The role of propagule pressure in explaining species invasions. Trends in Ecology and Evolution 20:223–228

Lodge DM (1993) Biological invasion: lessons for ecology. Trends in Ecology and Evolution 8:133–137

Lodge DM, Williams S, Macisaac HJ, Hayes KR, Leung B, Reichard S, Mack N, Moyle PB, Smith M Andow DA, Carlton JT, Mcmichael A (2006) Biological invasions: recommendations for US policy and management. Ecological Applications 16:2035–2054

Loi A, Howieson JG, Cocks PS, Caredda S (1993) The adaptation of *Medicago polymorpha* to a range of edaphic and environmental conditions: effect of temperature on growth, and acidity stress on nodulation and nod gene induction. Australian Journal of Experimental Agriculture 33:25–30

Lonsdale WM (1999) Global patterns of plant invasions and the concept of invasibility. Ecology 80:1522–1536

López JA, López P, López L, Cerrillo E, González A, Prada A (2007) Origen prehistórico de la dehesa en Extremadura: Una perspectiva paleoambiental. Revista de Estudios Extremeños 63:493-510

Lortie CL, Aarssen LW (1996) The specialization hypothesis for phenotypic plasticity in plants. International Journal of Plant Sciences 157:484–487

Lowe S, Browne M, Boudjelas S, De Poorter M (2000) 100 of the world's worst invasive alien species: a selection from the global invasive species database (p. 12). Auckland, New Zealand: Invasive Species Specialist Group

Luebert F, Pliscoff P (2006) Sinopsis bioclimática y vegetacional de Chile. Editorial Universitaria, Santiago de Chile, Chile

Lugo A, Gonzalez G (2010) Changing conditions and changing ecosystems: a long-term regional and transcontinental research approach on invasive species, 121–126. Gen. Tech. Rep. WO-79. U.S. Department of Agriculture, Forest Service. Washington, D.C. (USA)

Luken JO, Thieret JW (1997) Assessment and Management of Plant Invasions. Springer, New York

MA (Millennium Ecosystem Assessment) (2003) Ecosystems and human well-being: a framework for assessment. Island Press, Washington DC

MA (Millennium Ecosystem Assessment) (2005) Ecosystem and human well-being: Synthesis. Washington, DC. (USA)

MA (Millennium Ecosystem Assessment) (2012) MA. (2012)

MacDougall AS, Turkington R (2005) Are invasive species the drivers or passengers of change in degraded ecosystems? Ecology 86:42–55

Mace GM (2014) Whose conservation. Science 345:1558–1560

Mace GM, Norris K, Fitter AH (2012) Biodiversity and ecosystem services: a multilayered relationship. Trends in Ecology and Evolution 27:19–26

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Applications 10:689–710

Madrigal J, Kelt DA, Meserve PL, Gutiérrez JR, Squeo FA (2011) Bottom-up control of consumers leads to top-down indirect facilitation of invasive annual herbs in semiarid Chile. Ecology 92:282–288

Magro S, Jiménez MD, Casado MA, Mola I, Arenas JM, Martín-Duque JF, Vázquez A, Balaguer L (2014) Community ontogeny at the roadside: Critical life-cycle events throughout a sequential process of primary colonization. Applied Vegetation Science 17:493–503

Malo J, Suárez F (1997) Dispersal mechanism and transcontinental naturalization proneness among Mediterranean herbaceous species. Journal of Biogeography 24:391–394

Malone TF, Roederer JG (1984) Global change. Cambridge.

Máltez-Mouro S, Maestre F, Freitas H (2010) Co-occurrence patterns and abiotic stress in sand-dune communities: Their relationship varies with spatial scale and the stress estimator. Acta Oecologica 36:80–84

MAPA (Ministerio de Agricultura, Pesca y Alimentación) (2008) Diagnóstico de las Dehesas Ibéricas Mediterráneas. Tragsatec

Marañón T (1988) Agro-sylvo-pastoral systems in the Iberian Peninsula: *dehesas* and *montados*. Rangelands 10:255–258

Marañón T, Pugnaire TI, Callaway M (2009) Mediterranean-climate oak savannas: The interplay between abiotic environment and species interactions. Web Ecology 9:30–43

Margalef R (1975) Ecología. Omega, Barcelona

Marini L, Battisti A, Bona E, Federici G, Martini F, Pautasso M, Hulme PE (2012) Alien and native plant life-forms respond differently to human and climate pressures. Global Ecology and Biogeography 21:534–544

Marini M, Bertolli A, Bona E, Federici G, Martini F, Prosser F, Bommarco R (2013) Beta-diversity patterns elucidate mechanisms of alien plant invasion in mountains. Global Ecology and Biogeography 22:450–460

Maron JL, Vilà M, Bommarco R, Elmendorf S, Beardsley P (2004) Rapid evolution of an invasive plant. Ecological Monographs 74:261–280

Maron JL, Elmendorf SC, Vilà M (2007) Contrasting plant physiological adaptation to climate in the native and introduced range of Hypericum perforatum. Evolution 61:1912–1924

Marticorena C, Quezada M (1985) Catálogo de la flora vascular de Chile. Gayana Botanica 42:5–157

Marticorena C, Quezada M (1987) Adiciones a la flora de Chile. Gayana Botanica 44:39–44

Marticorena C, Rodríguez R (1995) Flora de Chile, I: Pteridophyta-Gymnospermae. Universidad de Concepción. Concepción. (Chile)

Marticorena C, Rodríguez R (2001) Flora de Chile, 2: Winteraceae-Ranunculaceae. Universidad de Concepción. Concepción. (Chile)

Martin LM, Wilsey BJ (2012) Assembly history alters alpha and beta diversity, exotic–native proportions and functioning of restored prairie plant communities. Journal of Applied Ecology 49:1436-1445

Martín-Forés I, Casado MA, Castro I, Ovalle C, del Pozo A, Acosta-Gallo B, Sánchez-Jardón L, de Miguel JM (2012) Flora of the Mediterranean basin in the Chilean *espinales*: evidence of colonization. Pastos 42:135–158

Martín-Forés I, Sánchez-Jardón L, Acosta-Gallo B, del Pozo A, Castro I, de Miguel JM, Ovalle C, Casado MA (2015) From Spain to Chile: environmental filters and success of herbaceous species in Mediterranean-climate regions. Biological invasions 17:1425–1438

Martín-López B, Gómez-Baggethun E, González JA, Lomas PL, Montes C (2009) the assessment of ecosystem services provided by biodiversity: re-thinking concepts and research needs. In: Aronoff JB (Ed.) Handbook of Nature Conservation: Global, Environmental and Economic Issues. Nova Science Publisher Inc, 479pp

Martín-López B, Montes C (2015) Restoruing the human capacity for conserving biodiversity: a social-ecological approach. Sustainability science (in press) doi: 10.1007/s11625-014-0283-3

Matthei O (1995) Manual de las malezas que crecen en Chile. Alfabeta Impresores. Santiago (Chile)

Mazerolle MJ. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). http://cran.r-project.org/web/packages/AICcmodavg/index.html. R package 1.35. 2013.

McCreadie JW, Bedwell CR (2013) Patterns of co-occurrence of stream insects and an examination of a causal mechanism: ecological checkerboard or habitat checkerboard? Insect Conservation and Diversity 6:105-113

McDowell SCL (2002) Photosynthetic characteristics of invasive and non-invasive species of *Rubus* (Rosaceae). American Journal of Botany 89:1431—1438

McEvoy PB (1984) Dormancy and dispersal in dimorphic achenes of tansy ragwort *Senecio jacobaea*. Oecologia 61:160—168

McGeoch MA, Butchart SHM, Spear D, Marais E, Kleynhans EJ, Symes A, Chanson J, Hoffmann M (2010) Global indicators of biological invasion: species numbers, biodiversity impact and policy responses. Diversity and Distributions 16:95—108

McKinney ML, Lockwood JL (2001) Biotic homogenization: a sequential and selective process. In: Lockwood JL, McKinney ML (Eds.) Biotic homogenization, 1-18. Kluwer Academic/Plenum Publishers. New York (USA)

McLane CR, Battaglia LL, Gibson DJ, Groninger WJ (2012) Succession of exotic and native species assemblages within restored floodplain forests: A test of the parallel dynamics hypothesis. Restoration Ecology 20:202—210

Meiners SJ (2007) Native and exotic plant species exhibit similar population dynamics during succession. Ecology 88:1098—1104

Meiners SJ, Pickett STA, Cadenasso ML (2001) Effects of plant invasions on the species richness of abandoned agricultural land. Ecography 24:633—644

Meiners SJ, Pickett STA, Cadenasso ML (2002) Exotic plant invasions over 40 years of old field successions: community patterns and associations. Ecography 25:215—223

Melbourne B, Cornell HV, Davies KF, Dugaw CJ, Elmendorf S, Freestone AL, Hall RJ, Harrison S, Hastings A, Holland M, Holyoak M, Lambrinos J, Moore K, Yokomizo H (2007) Invasion in a heterogeneous world: resistance, coexistence or hostile takeover? Ecology Letters 10:77—94

Meyerson LA, Mooney HA (2007) Invasive alien species in an era of globalization. Frontiers in Ecology and the Environment 5:199—208

Milchunas DG, Lauenroth WK (1993) Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecological Monographs 63:327—366

Molina-Montenegro MA, Atala C, Gianoliet, E (2010) Phenotypic plasticity and performance of Taraxacum officinale (dandelion) in habitats of contrasting environmental heterogeneity. Biological Invasions 12: 2277—2284

Molina-Montenegro MA, Naya DE (2012) Latitudinal patterns in phenotypic plasticity and fitness-related traits: assessing the climatic variability hypothesis (CVH) with an invasive plant species. PLoS One 7:e47620

Molina-Montenegro MA, Peñuelas J, Munné-Bosch S, Sardans J (2012) Higher plasticity in ecophysiological traits enhances the performance and invasion success of *Taraxacum officinale* (dandelion) in alpine environments. Biological Invasions 14: 21—33

Molina-Montenegro MA, Palma-Rojas C, Alcayaga-Olivares Y, Oses R, Corcuera LJ, Cavieres LA, Gianoliet E (2013) Ecophysiological plasticity and local differentiation help explain the invasion success of *Taraxacum officinale* (dandelion) in South America. Ecography 36: 718—730

Montenegro G, Teillier S, Arce P, Poblete V (1991) Introductions of plants and animals into the Mediterranean-type climate area of Chile. In: Groves RH, Di Castri F. Biogeography of Mediterranean invasions, 103-109. Eds. Cambridge University Press. Cambridge (UK)

Montes C, Santos Martín F, Benayas J, Gomez Sal A, Pineda FD (2014) Ecosystems and biodiversity for human wellbeing. Spanish National Ecosystems Assessment. Synthesis of key findings. Ministerio de Agricultura, Alimentación y Medio Ambiente (MAGRAMA). Madrid

Montoya JM (1983) Analisis, caracterizacion, optimizacion y gestion integrada de los recursos paisajisticos agrarios (hombre y sistema). Instituto Nacional de Investigaciones Agrarias Nº 20. Madrid

Moore JL, Mouquet N, Lawton JH, Loreau M (2001) Coexistence, saturation and invasion resistance in simulated plant assemblages. Oikos 94:303—314

Mossman RE (2009) Seed dispersal and reproduction patterns among everglades plants. FIU Electronic Theses and Dissertations. Paper 135.

Muñoz MR, Fuentes ER (1989) Does fire induce shrub germination in the Chilean matorral? Oikos 56: 177—181

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853—858

Naeem S, Bunker DE, Hector A, Loreau M, Perrings C (2009) Biodiversity, ecosystem functioning and human wellbeing: An Ecological and Economic Perspective. Oxford: Oxford University Press, UK

National Geographic Society (1991) 1491: America Before Columbus. William Reese Company. 154 pp

Naveh Z (2000) What is holistic landscape ecology? A conceptual introduction. Landscape and urban planning 50:7—26

Neuffer B (1990) Ecotype differentiation in *Capsella*. Vegetatio 89:165—171

Niinemets Ü, Valladares F, Ceulemans R (2003) Leaf-level phenotypic variability and plasticity of invasive *Rhododendron ponticum* and non-invasive *Ilex*

aquifolium co-occurring at two contrasting European sites. Plant Cell and Environment 26:941–956

Ninyerola M, Pons X, Roure JM (2005) Atlas Climático Digital de la Península Ibérica. Metodología y aplicaciones en bioclimatología y geobotánica. ISBN 932860-8-7. Universidad Autónoma de Barcelona, Bellaterra. http://opengis.uab.es/wms/iberia/index.htm

Noble IR (1989) Attributes of invaders and the invading process: terrestrial and vascular plants. Biological invasions: a global perspective. Wiley, Chichester, 301-313

Norton JB, Monaco TA, Norton U (2007) Mediterranean annual grasses in western North America: kids in a candy store. Plant and Soil 298:1–5

Olden JD, Rooney TP (2006) On defining and quantifying biotic homogenization. Global Ecology and Biogeography 15:113-120

Olden, JD (2006) Biotic homogenization: a new research agenda for conservation biogeography. Journal of Biogeography 33:2027-2039

Olivares EA, Gastó CJ (1971) Comunidades de terófitos en subseres postaradura y en exclusión en la estepa de *Acacia caven* (Mol.) Hook et Arn. Boletín Técnico nº 34, Universidad de Chile, Facultad de Agronomía. Santiago (Chile)

Ormazabal C (1993) The conservation of biodiversity in Chile. Revista Chilena de Historia Natural 66:383–402

Orrock JR, Witter MS, Richman OJ (2008) Apparent competition with an exotic plant reduces native plant establishment. Ecology 89:1168–1174

Ovalle C, Avendaño J (1987) Interactions de la strate ligneuse avec la strate herbacée dans les formations d'*Acacia caven* (Mol.) Hook et Arn. au Chili. Oecologia Plantarum 8:385–404

Ovalle C, Avendaño J, Muñoz M, Serra MT (1987) Herbario de la vegetación natural mediterráneo de la zona del secano interior de Cauquenes, 117-118. Área de Producción Animal. Estación Experimental Quilamapu (INIA). Informe Técnico 1986/87. Chillán (Chile)

Ovalle C, Aronson J, Del Pozo A, Avendaño J (1990) The *espinal*: Agroforestry systems of the Mediterranean-type climate region of Chile. Agroforestry Systems 10:213–239

Ovalle C, Avendaño J, del Pozo A, Aronson J (1996) Land occupation patterns and vegetation structure of the anthropogenic savannas (*espinales*) of central Chile. Forest Ecology and Management 86:129-139

Ovalle C, Aronson J, Del Pozo A, Avendaño J (1999) Restoration and rehabilitation of mixed *Espinales* in Central Chile: 10-year report and appraisal. Arid Soil Research and Rehabilitation 13:369-381

Ovalle C, Del Pozo A, Casado MA, Acosta B, De Miguel JM (2005) Consequences of landscape heterogeneity on grassland diversity and productivity in the *Espinal* agroforestry system of Central Chile. Landscape Ecology 21:585–594

Ovalle C, Del Pozo A, Casado MA, Acosta B, De Miguel JM (2006) Consequences of landscape heterogeneity on grassland diversity and productivity in the *espinal* agroforestry system of central Chile. Landscape Ecology 21:585–594

Palang H, Mander Ü, Naveh Z (2000) Holistic landscape ecology in action. Landscape and Urban Planning 50:1–6

Parker IM, Rodriguez J, Loik ME (2003) An evolutionary approach to understanding the biology of invasions: Local adaptation and general-purpose genotypes in the weed *Verbascum thapsus*. Conservation Biology 17:59–72

Parsons DJ (1976) Vegetation structure in Mediterranean communities of California and Chile. Journal of Ecology 64: 435–447

Paskoff R, Manríquez H (1999) Ecosystem and legal framework for coastal management in central Chile. Ocean and Coastal Management 42:105–117

Pauchard A, Alaback PB (2004) Influence of elevation, land use, and landscape context on patterns of alien plant invasions along roadsides in protected areas of south-central Chile. Conservation Biology 18:238–248

Pauchard A, Cavieres L, Bustamante R (2004) Comparing alien plantinvasions amongregions withsimilarclimates: where to from here? Diversity and Distributions 10:371–375

Pauchard A, Aguayo M, Peña E, Urrutia R (2006) Multiple effects of urbanization on the biodiversity of developing countries: the case of a fast-growing metropolitan area (Concepción, Chile). Biological Conservation 127:272–281

Pauchard A, Keuffer C, Dietz H, Daehler CC, Alexander JM, Edwards PJ, Arévalo JR, Cavieres LA, Guisan A, Haider S, Jakobs G, McDougall KL, Millar IC, Naylor BJ, Parks CG, Rew LJ, Seipel T (2009) Ain't no mountain high enough: Plant invasions reaching new elevations. Frontiers in Ecology and the Environment 7:479–486

Patel S (2011) A weed with multiple utility: *Lantana camara*. Reviews in Environmental Science and Bio/Technology 10:341–351

Peco B (1989) Modelling Mediterranean pastures dynamics. Vegetatio 83:269–273

Peco B, Levassor C, Casado MA, Galiano EF, Pineda FD (1983) Influences météorologiques et géomorphologiques sur la succession de pâturages de thérophytes méditerranéennes. Ecologia Mediterranea 9:63–76

Pejchar L, Mooney HA (2009) Invasive species, ecosystem services and human well-being. Trends in Ecology and Evolution 24:495–504

Pereira HM, Domingos T, Vicente L (2004) Portugal millennium ecosystem assessment: state of the assessment report. Centro de Biologia Ambiental, Faculdade de Ciências da Universidade de Lisboa, Lisboa

Peres-Neto PR (2004) Patterns in the co-occurrence of fish species in streams: the role of site suitability, morphology and phylogeny versus species. Oecologia 140:352-360

Perevolotsky A, Seligman NG (1998) Role of grazing in Mediterranean rangeland ecosystems – inversion of a paradigm. BioScience 48:1007–1017

Perrings C, Dehnen-Schmutz K, Touza J & Williamson M (2005) How to manage biological invasions under globalization. Trends in Ecology and Evolution 20:212–215

Piano E, Pecetti L, Carroni AM (1996) Climatic adaptation in subterranean clover populations. Euphytica 92:39–44

Pienkowski T, Williams S, McLaren K, Wilson B, Hockley N (2015) Alien invasions and livelihoods: Economic benefits of invasive Australian Red Claw crayfish in Jamaica. Ecological Economics 112:68–77

Pieterse JN (1994) Globalisation as hybridisation. International Sociology 9:161-184

Pieterse JN (2015) Globalization and Culture: Global Mélange. Lanham MD, Rowman & Littlefield, USA, 219pp

Pimentel D, Lach L, Zuniga R, Morrison D (1999) Environmental and economic costs associated with introduced nonnative species in the United States. Manuscript, pp 1 –28

Pimentel D , McNair S, Janecka J, Wightman J, Simmonds C, O'Connell C, Wong E, Russel L, Zern J, Aquino T, Tsomondo T (2001) Economic and environmental threats of alien plant, animal, and microbe invasions. Agriculture, Ecosystems and Environment 84:1–20

Pimentel D, Zuniga R, Morrison D (2005). Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological Economics 52:273–288

Pineda FD (1990) Perspectives on research into Spanish open woodlands (*dehesa*): some recent ecological experiences. Plant Biosystem 124:311-320

Pineda FD, Acosta-Gallo B (2012) Bosque y matorral esclerófilo mediterráneo. In: Montes C, Benayas J, Torres I, Aymerich M, Artola M, Pineda FD, Gómez Sal A (Coords.). Evaluación de los Ecosistemas del Milenio de España. Fundación Biodiversidad, Mº Medio Ambiente, Madrid. Capítulo 5: 13–92

Pineda FD, Montalvo J (1995) *Dehesa* systems in the western Mediterranean. In: Halladay P, Golmour DA (Eds.) Conserving biodiversity outside protected areas. IUCN, Cambridge, pp 107–122

Pineda FD, Nicolas JP, Pou A, Galiano EF (1981) Ecological succession in oligotrophic pastures of central Spain. Vegetatio 44:165–176

Pineda FD, Schmitz MF, Hernández S (2002) Interacciones entre infraestructuras y conectividad natural del paisaje. I Congreso Ingeniería Civil, Territorio y Medio Ambiente. Col. Ing. CC y Puertos, Madrid

Pineda FD (Coord), Schmitz MF, Acosta-Gallo B, Fernández Pastor M, Arnaiz C, Díaz P, Ruiz-Labourdette D (2014) Informe y síntesis de la actividad investigadora desarrollada en el marco de la Red de Seguimiento del Cambio Global (RSCG) en los Parques Nacionales españoles (RPN). Fundación Biodiversidad. Convenio Organismo Autónomo Parques Nacionales (OAPN)- Oficina Española del Cambio Climático (OECC)- Fundación Biodiversidad (FB)- Agencia Española de Meteorología (AEMT). Madrid

Prach K, Walker LR (2011) Four opportunities for studies of ecological succession. Trends in Ecology and Evolution 26:119–123

Preston CD, Pearman DA & Hall AR (2004) Archaeophytes in Britain. Botanical Journal of the Linnean Society 145:257–294

Priestley DA (1986) Seed aging, implications for seed storage and persistence in the soil. Cornell University Press, New York

Prinzing A, Durka W, Klotz S, Brandl R (2002) Which species become aliens? Evolutionary Ecology Research 4:385–405

Pyšek P (1998) Is there a taxonomic pattern to plant invasions? Oikos 82:282–294

Pyšek P, Chytrý M (2014) Habitat invasion research: where vegetation science and invasion ecology meet. Journal of Vegetation Science 25:1181-1187

Pyšek P, Jarošík V, Chytrý M, Kropáč ZK, Tichý L, Wild J (2005) Alien plants in temperate weed communities: prehistoric and recent invaders occupy different habitats. Ecology 86:772-785

Pyšek P, Richardson DM, Williamson M (2004) Predicting and explaining plant invasions through analysis of source area floras: some critical considerations. Diversity and Distributions 10:179–187

Pyšek P, Richardson DM (2006) The biogeography of naturalization in alien plants. Journal of Biogeography 33:2040-2050

Pyšek P, Richardson DM (2007) Traits associated with invasiveness in alien plants: where do we stand? In: Nentwig W (ed) Biological invasions, ecological studies 193. Springer, Berlin and Heidelberg, pp 97–126

Pyšek P, Krivanek M, Jarošík V (2009a) Planting intensity, residence time, and species traits determine invasion success of alien woody species. Ecology 90:2734–2744

Pyšek P, Jarošík V, Pergl J, Randall R, Chytrý M, Kühn I, Tichý L, Danihelka J, Chrtek J, Sádlo J (2009b) The global invasion success of Central European plants is related to distribution characteristics in their native range and species traits. Diversity and Distributions 15:891–903

Pyšek P, Jarošík V, Hulme PE, Kühn I, Wild J, Arianoutsou M, Bacher S, Chiron F, Didžiulis V, Essl F, Genovesi P, Gherardi F, Hejda M, Kark S, Lambdon PW, Desprez-Loustau ML, Nentwig W, Pergl J, Poboljšaj K, Rabitsch W, Roques A, Roy DB, Shirley S, Solarz W, Vilà M, Winter M (2010) Disentangling the role of environmental and human pressures on biological invasions across Europe. Proceedings of the National Academy of Sciences of the United States of America 107:12157–12162

Pyšek P, Richardson DM (2010) Invasive species, environmental change and management, and health. Annual Review of Environment and Resources 35:25-55

Pyšek P, Jarošík V, Pergl J (2011) Alien plants introduced by different pathways differ in invasion success: Unintentional introductions as a threat to natural areas. PLOS ONE 6:1–11

Quintanilla PV (1981) Carta de las formaciones vegetales de Chile. Contribuciones científicas y tecnológicas, Universidad Técnica del Estado Nº 47. 32 pp. Santiago (Chile)

R Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Reale O, Dirmeyer P (2000) Modeling the effects of vegetation on Mediterranean climate during the Roman Classical Period – Part I: climate history and model sensitivity. Global Planet 25:163–184.

Reale O, Shukla J (2000) Modeling the effects of vegetation on Mediterranean climate during the Roman Classical Period: Part II: model simulation. Global Planet 25:185—214.

Reiche K (1896-1911) Flora de Chile, 381, 397, 427, 489, 463, 176 pp. Santiago (Chile)

Reitalu T, Prentice HC, Sykes MT, Lönn M, Johansson LJ, Hall K (2008) Plant species segregation on different spatial scales in semi-natural grasslands. Journal of Vegetation Sciences 19:407—416

Rejmánek M, Robinson GR, Rejmankova E (1989) Weed-crop competition - experimental-designs and models for data-analysis. Weed Science 37:276-284

Rejmánek M, Thomsen CD, Peters ID (1991) Invasive vascular plants of California. In: Groves RH, Di Castri F (Eds.) Biogeography Of Mediterranean Invasions, 81—101. Cambridge University Press. Cambridge (UK)

Rejmánek M, Richardson DM, Higgins SI, Pitcairn MJ, Grotkopp E (2005) Ecology of invasive plants: state of the art. In: Mooney HA, Mack RN, McNeely JA, Neville LE, Schei PJ, Waage JK (Eds.) Invasive alien species a new synthesis. Island Press, Washington DC, pp 104—161

Rejmánek M, Richardson DM, Pyšek P (2013) Plant invasions and invasibility of plant communities. In: van der Maarel E, Franklin J (eds) Vegetation ecology, Second Edition, John Wiley & Sons, Ltd, Oxford, UK

Richards CL, Bossdorf O, Muth NZ, Gurevitch J, Pigliucci M (2006) Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. Ecoogyl Letters 9:981—993

Richardson DM, MacDonald IAW, Firsyth GG (1989) Reductions in plant species richness under stands of exotic trees and shrubs in the fynbos biome. South African Forestry Journal 149:1—8

Richardson DM, Pyšek P, Rejmánek M, Barbour MG, Panetta FD, West CJ (2000) Naturalization and invasion of naturalized plants: concepts and definitions. Diversity and Distributions 6:93—107

Richardson DM, Pyšek P (2006) Plant invasions: merging the concepts of species invasiveness and community invasibility. Progress in Physical Geography 30:409—431

Richardson DM, Holmes PM, Esler KJ, Galatowitsch SM, Stromberg JC, Kirkman SP, Pyšek P, Hobbs RJ (2007) Riparian vegetation: degradation, exotic plant invasions, and restoration prospects. Diversity and Distributions 13:126—139

Richardson DM, Carruthers J, Hui C, Impson FA, Miller JT, Robertson MP, Rouget M, Le Roux JJ, Wilson JR (2011) Human-mediated introductions of Australian acacias —a global experiment in biogeography. Diversity and Distributions 17: 771-787

Richardson DM, Pyšek P (2012) Naturalization of introduced plants: ecological drivers of biogeographical patterns. New Phytologist 196:383—396

Richardson DM, Hui C, Nuñez MA, Pauchard A (2014) Tree invasions: patterns ,processes, challenges and opportunities. Biological Invasions 16: 473-481

Richerson PJ, Lum K (1980) Patterns of plant species diversity in California—relation to weather and topography. American Naturalist 116:504—536

Ricklefs R (2004) A comprehensive framework for global patterns in biodiversity. Ecology Letters 7:1—15

Ricotta C, La Sorte FA, Pyšek P, Rapson GL, Celesti-Grapow L, Thompson K (2009) Phyloecology of urban alien floras. Journal of Ecology 97:1243—1251

Rivas-Martínez S, Díaz TE, Fernández-González F, Izco J, Loidi J, Lousã M, Penas A (2002) Vascular plant communities of Spain and Portugal. Addenda to the syntaxonomical checklist of 2001. Itinera Geobotanica 15:5—922

Rockstrom J, Steffen W, Noone K, Persson Å, Chapin Iii FS, Lambin EF, Lenton TM Scheffer M, Folke C, Schellnhuber HJ, Nykvist B, De Wit CA, Huges T, Van Der Leeuw S, Rodhe H, Sörlin S, Snyder PK, Costanza R, Svedin U, Falkenmark M, Karlberg L, Corell RW, Fabry VJ, Hansen J, Walker B, Liverman D, Richardson K, Crutzen P, Foley JA (2009) A safe operating space for humanity. Nature 461:472-475

Rodríguez E, Mattei S, Quezada M (1983) Flora arbórea de Chile. Ed. Universidad de Concepción, 408 p. Chillán (Chile)

Rodríguez LF (2006) Can invasive species facilitate native species? Evidence of how, when, and why these impacts occur. Biological Invasions 8:927-939

Rouget M, Richardson DM, Cowling RM, Lloyd JW, Lombard AT (2003) Current patterns of habitat transformation and future threats to biodiversity in terrestrial ecosystems of the Cape Floristic Region, South Africa. Biological Conservation 112:63—85

Rouget M, Hui C, Renteria J, Richardson DM, Wilson JRU (2015) Plant invasions as a biogeographical assay: Vegetation biomes constrain the distribution of invasive alien species assemblages, South African Journal of Botany (in press) doi: 10.1016/j.sajb.2015.04.009

Ruíz Pérez M (1986) Sustainable food and energy production in the Spanish *Dehesa*. UNU-Food and Energy Nexus Program. The United Nations University, Paris

Rundel PW (1998) Landscape disturbance in Mediterranean type ecosystems: an overview. In: Rundel PW, Montenegro G, Jaksic FM (Eds.) Landscapes disturbance and biodiversity in Mediterranean-type ecosystems. Springer, Germany, pp 3—22

Sadzawka A, Carrasco MA, Grez R, Mora ML, Flores H, Neaman A (2006) Métodos de análisis recomendados para los suelos de Chile. Revisión 2006. Instituto de Investigaciones Agropecuarias, Serie Actas INIA N8 34, Santiago, Chile

Sala OE, Chapin FS , III, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, LeRoy Poff N, Sykes MT, Walker BH, Walker M, Wall DH (2000) Global biodiversity scenarios of the year 2100. Science 287:1770—1774

Sáiz F, Ojeda P (1988) *Oryctolagus cuniculus* L. en Juan Fernández: problema y control. Anales del Museo de Historia Natural de Valparaíso (Chile) 14:197-215

Sanders NJ, Gotelli NJ, Heller NE, Gordon DM (2003) Community disassembly by an invasive species. Proceedings of the National Academy of Sciences

of the United States of America 100:2474—2477

Saul WC, Jeschke JM, Heger T (2013) The role of eco-evolutionary experience in invasion success. NeoBiota 17:57—74

Sax DF (2001) Latitudinal gradients and geographic ranges of exotic species: implications for biogeography. Journal of Biogeography 28:139—150

Sax DF, Brown JH (2000) The paradox of invasion. Global Ecology and Biogeography 9:363—372

Sax DF, Gaines SD, Brown JH (2002) Species invasions exceed extinctions on islands worldwide: a comparative study of plants and birds. The American Naturalist 160:766—783

Sax DF, Gaines SD (2008) Species invasions and extinction: The future of native biodiversity on islands. Proceedings of the National Academy of Sciences of the United States of America 105:11490—11497

Schellnhuber HJ, Crutzen PJ, Clark WC, Hunt J (2005) Earth system analysis for sustainability. Environment: Science and Policy for Sustainable Development 47:10—25

Schlaepfer MA, Sax DF, Olden JD (2011) The potential conservation value of nonnative species. Conservation Biology 25:428—437

Schlaepfer MA, Sax DF, Olden JD (2012) Toward a More Balanced View of Non- Native Species. Conservation Biology 26:1156

Schmitz MF, Pineda FD, Castro H, de Aranzabal I, Aguilera P (2005) Cultural landscape and socioeconomic structure. Environmental value and demand for tourism in a Mediterranean territory. Junta de Andalucía. Sevilla

Schwartz MW, Thorne JH, Viers JH (2006) Biotic homogenization of the California flora in urban and urbanizing regions. Biological Conservation 187:282—291

Seastedt TR, Hobbs RJ, Suding KN (2008) Management of novel ecosystems: are novel approaches required?. Frontiers in Ecology and the Environment 6:547—553

Seipel T, Kueffer C, Rew LJ, Kueffer C, Rew LJ, Daehler CC, Pauchard A, Naylor BJ, Alexander JM, Edwards PJ, Parks CG, Arevalo JR, Cavieres LA, Dietz H, Jakobs G, McDougall K, Otto R, Walsh N (2012) Processes at multiple scales affect richness and similarity of non-native plant species in mountains around the world. Global Ecology and Biogeography 21:236—246

Shackleton CM, McGarry D, Fourie S, Gambiza J, Shackleton SE, Fabricius C (2006) Assessing the effects of invasive alien species on rural livelihoods: case examples and a framework from South Africa. Human Ecology 35:113—127.

Shackleton S, Delang C, Angelsen A (2011a) From Subsistence to Safety Nets and Cash Income: Exploring the Diverse Values of Non-timber Forest Products for Livelihoods and Poverty Alleviation in Non-Timber Forest Products in the Global Context. In: Shackleton S, Shackleton C, Shanley P (Eds.) Springer Berlin Heidelberg, Berlin, Heidelberg

Shackleton S, Kirby D, Gambiza J (2011b) Invasive plants — friends or foes? Contribution of prickly pear (*Opuntia ficus-indica*) to livelihoods in Makana Municipality, Eastern Cape, South Africa. Development Southern Africa 28:177—193

Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. Trends in Ecology and Evolution 17:170—176

Sher AA, Hyatt LA (1999) The disturbed resource-flux invasion matrix: a new framework for patterns of plant invasion. Biological Invasions 1:107—114

Simberloff D (1995) Why do introduced species appear to devastate islands more than mainland areas? Pacific Science 49:87—97

Simberloff D, Von Holle B (1999) Positive interactions of nonindigenous species: invasional meltdown? Biological Invasions 1:21—32

Simberloff D, Parker IM, Windle PN (2005) Introduced species policy, management, and future research needs. Frontiers in Ecology and the Environment 3:12—20

Small E, Lefkovich LP (1986) Relationships among morphology, geography and infertility in *Medicago.* Canadian Journal of Botany 11:41—76

Solbrig OT, Cody ER, Fuentes ZW, Glanz JH, Moldenke AR (2000) The origin of biota. In: Mooney HA (Ed.) Convergent Evolution in Chile and California. Mediterranean Climate Ecosystems. Dowden, Hutchinson and Ross. Stroudsburg, USA

Sorensen AE (1978) Somatic polymorphism and seed dispersal. Nature (London) 276:174—176

Statgraphics Centurion, X. V. I. (2013). Statgraphics centurion XVI software version 16.2.04. Warrenton: StatPoint Technologies Inc.

Stone L, Roberts A (1990) The checkerboard score and species distributions. Oecologia 85:74-79

Steffen W, Andreae MO, Bolin B, Cox PM, Crutzen PJ, Cubasch U, Held H, Nakicenovic N, Scholes RJ, Talaue-McManus L, Turner II BL (2004) The Achilles'heels of the Earth System. Environment 46:9-20

Strayer DL, Eviner VT, Jeschke JM, Pace ML (2006) Understanding the long-term effects of species invasions. Trends in Ecology and Evolution 21:645—651

Suding KN, Gross KL, Houseman GR (2004) Alternative states and positive feedbacks in restoration ecology. Trends in Ecology and Evolution 19:46—53

Sultan SE (2000) Phenotypic plasticity for plant development, function and life history. Trends in Plant Science 5:537-542

Sutherland WJR, Freckleton RP, Godfray HCJ, Beissinger SR, Benton T, Cameron DD, Carmel Y, Coomes DA, Coulson T, Emmerson MC, Hails RS, Hays GC, Hodgson DJ, Hutchings MJ, Johnson D, Jones JPG, Keeling MJ, Kokko H, Kunin WE, Lambin X, Lewis OT, Malhi Y, Mieszkowska N, Milner-Gulland EJ, Norris K, Phillimore AB, Purves DW, Reid JM, Reuman DC, Thompson K, Travis JMJ, Turnbull LA, Wardle DA, Wiegand T (2013) Identification of 100 fundamental ecological questions. Journal of Ecology 101:58—67

Tecco PA, Díaz S, Cabido M, Urcelay C (2010) Functional traits of alien plants across contrasting climatic and land-use regimes: do aliens join the locals or try harder than them? Journal of Ecology 98:17—27

Thompson K, Hodgson JG, Rich TC (1995) Native and alien invasive plants: more of the same? Ecography 18:390-402.

Thomsen MA, D'Antonio CM, Suttle KB, Sousa WP (2006) Ecological resistance, seed density and their interactions determine patterns of invasion in a Californian coastal grassland. Ecology Letters 9:160–170

Thuiller W, Richardson DM, Py šek P, Midgley GF, Hughes GO, Rouget M (2005) Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. Global Change Biology 11:2234–2250

Tiffney BH (1984) Seed size, dispersal syndromes, and the rise of the angiosperms: evidence and hypothesis. Annals of the Missouri Botanical Garden 71. Historical Perspectives of Angiosperm Evolution, pp 551-576

Tilman D (1997) Community invasibility, recruitment limitation, and grassland biodiversity. Ecology 78:81–92

Tognetti PM, Chaneton EJ, Omacini M, Trebino HJ, León RJC (2010) Exotic vs. native plant dominance over 20 years of old field succession on set aside farmland in Argentina. Biological Conservation 143:2494–2503

Tognetti PM, Chaneton EJ (2012) Invasive exotic grasses and seed arrival limit native species establishment in an old-field grassland succession. Biological Invasions 14:2531–2544

Trabaud L (1991) Is fire an agent favouring plant invasions? In: Groves RH, Di Castri F (Eds.) Biogeography of Mediterranean Invasions. 179–189. Cambridge University Press. Cambridge (UK)

Turner BL, Gómez Sal A, González Bernáldez F, Di Castri F (Eds.) (1995) Global Land Use Change. A Perspective from the Columbian Encounter. CSIC. Madrid (España).

Tutin TG, Burges NA, Chater AO, Edmondson JR, Heywood VH, Moore DM, Valentine DH, Walters SM, Webb DA (1964–1980) Flora Europea, vols. 1–5. Ed. University Press, Cambridge Underwood EC

Turner BL, Gómez Sal A, González Bernáldez F, Di Castri F (Eds.) (1995) Global Land Use Change. A Perspective from the Columbian Encounter. CSIC, Madrid, España

Ulrich W, Gotelli NJ (2013) Pattern detection in null model analysis. Oikos 122:2-18

Underwood EC, Viers JH, Klausmeyer KR, Cox RL, Shaw R (2009) Threats and biodiversity in the Mediterranean biome. Diversity and Distributions 15:188-197

USDA (2006) Forest Service resource planning assessment report. Interim update of the 2000 RPA assessment. U.S. Department of Agriculture. Forest Service. Washington, DC (USA)

Valladares F, Dobarro I, Sánchez-Gómez D, Pearcy RW (2005) Photoinhibition and drought in Mediterranean woody saplings: scaling effects and interactions in sun and shade phenotypes. Journal of Experimental Botany 56:483–494

Van de Wouw P, Echeverría C, Rey-Benayas JM, Holmgren M (2011) Persistent *Acacia* savannas replace Mediterranean sclerophyllous forests in South America. Forest Ecology and Management 262:1100–1108

van Kleunen M, Dawson W, Schlaepfer D, Jeschke JM, Fischer M (2010a) Are invaders different? A conceptual framework of comparative approaches for assessing determinants of invasiveness. Ecology Letters 13:947–958

van Kleunen M, Weber E, Fischer M (2010b) A meta-analysis of trait differences between invasive and non-invasive plant species. Ecology Letters 13: 235–245

Van Riel P, Jordaens K, Martins AMF, Backeljau T (2000) Eradication of exotic species. Trends in Ecology and Evolution 15:515

van Wilgen BW, de Wit MP, Anderson HJ, le Maitre DC, Kotze IM, Ndala S, Brown B, Rapholo MB (2004) Costs and benefits of biological control of invasive alien plants: case studies from South Africa. South African Journal of Sciences 100:113–122

Veblen, TT, Lorenz DC (1988) Recent vegetation changes along the forest/steppe ecotone of northern Patagonia. Annals of the Association of American Geographers 78:93–111

Veech JA (2013) A probabilistic model for analyzing species co-occurrence. Global Ecology and Biogeography 22:252-260

Velasco D, García-Llorente M, Alonso B, Dolera A, Palomo I, Iniesta-Arandia I, Martín-López B (2015) Biodiversity conservation research challenges in the 21st century: A review of publishing trends in 2000 and 2011. Environmental Science and Policy 54:90–96

Venable DL (1985) The evolutionary ecology of seed heteromorphism. The American Naturalist 126:577–595

Venable DL, Brown JS (1988) The selective interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. The American Naturalist 131:360-384

Venable DL, Lawlor L (1980) Delayed germination and dispersal in desert annuals: escape in space and time. Oecologia 46:272–282

Venable DL, Burquez AM, Corral G, Morales E, Espinosa F (1987) The ecology of seed heteromorphism on *Heterosperma pinnatum* in Central Mexico. Ecology 68:65–76

Viers JH, Klausmeyer KR, Cox RL, Shaw R (2009) Threats and biodiversity in the Mediterranean biome. Diversity and Distributions 15:188–197

Villa-Martínez, R.; Villagrán, C.; Jenny, B., 2003. The last 7500 cal yr BP of westerly rainfall in Central Chile inferred from a high-resolution pollen record from Laguna Aculeo 34°S. Quaternary Research 60:284–293

Vitousek PM (1994) Beyond global warming: ecology and global change. Ecology 75:1861–1876

Vitousek PM, D'Antonio CM, Loope LL, Westbrooks R (1996) Biological Invasions as Global Environmental Change. American Scientist 84:468–478

Vitousek PM, D'Antonio CM, Loope LL, Rejmánek M, Westbrooks R (1997) Introduced species: a significant component of human-caused global change. New Zealand Journal of Ecology 21:1—1

Vilà M, Espinar JL, Hejda M, Hulme PE, Jarošík V, Maron JL, Perlg J, Schaffner U, Sun Y, Pyšek P (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecology Letters 14:702—708

Wade TG, Riitters KH, Wickham JD, Jones KB (2003) Distribution and causes of global forest fragmentation. Conservation Ecology 7:7

Walker LR, del Moral R (2003) Primary succession and ecosystem rehabilitation, Cambridge University Press

Weiher E, Keddy P (1999) Assembly rules as general constraints on community composition, in: Weither E, Keddy P (Eds.) Ecological assembly rules, perspectives, advances, and retreats. Cambridge University Press, Cambridge, pp. 251—271

Wiens JJ, Donoghue MJ (2004) Historical biogeography, ecology and species richness. Trends in Ecology and Evolution 19:639—644

Wiens JJ, Graham CH (2005) Niche conservatism: integrating evolution, ecology, and conservation biology. Annual Review of Ecology, Evolution and Systematics 36:519—539

Williamson M (1996) Biological invasions. Chapman and Hall, London

Wilson JRU, Richardson DM, Rouget M, Procheş Ş, Amis MA, Henderson L, Thuiller W (2007) Residence time and potential range: crucial considerations in modelling plant invasions. Diversity and Distributions 13:11—22

Wilson JRU, Dormontt ED, Prentis PJ, Lowe AJ, Richardson DM (2009) Something in the way you move: dispersal pathways affect invasion success. Trends in Ecology and Evolution 24:136—143

Winter M, Schweigera O, Klotza S, Nentwigc W, Andriopoulosd P, Arianoutsoud M, Basnoue C, Delipetrouf P, Didžiulisg V, Hejdah M, Hulmei PE, Lambdonj PW, Perglh J, Pyšek P, Royl DB, Kühna I (2009) Plant extinctions and introductions lead to phylogenetic and taxonomic homogenization of the European flora. Proceedings of the National Academy of Sciences of the United States of America 106:21721—21725

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, Flexas J, Garnier E, Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas ML, Niinemets U, Oleksyn J, Osada N, Poorter H, Poot P, Prior L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG, Veneklaas EJ, Villar R (2004) The worldwide leaf economics spectrum. Nature 428:821—827

Wu SH, Chaw SM, Rejmánek M (2003) Naturalized Fabaceae (Leguminosae) species in Taiwan: the first approximation. Botanical Bulletin of Academia Sinica 44:59—66

Young TP, Chase JM, Huddleston RT (2001) Community succession and assembly. comparing, contrasting and combining paradigms in the context of ecological restoration. Ecological Restoration 19:5—18

Young SL (2010) What contributions are invasive plant species making to ecosystem services? Journal of Soil and Water Conservation 65:31—32

Young SL (2012) Ecosystem services: the significance of contributions by invasive plant species. Invasive Plant Sciences Management 5:106—107

Young TP, Chase JM, Huddleston RT (2001). Community succession and assembly. comparing, contrasting and combining paradigms in the context of ecological restoration. Ecological Restoration 19:5—18

Zavaleta ES, Hobbs RJ, Mooney HA (2001) Viewing invasive species removal in a whole-ecosystem context. Trends in Ecology and Evolution 16:454—459

Zeder MA (2008) Domestication and early agriculture in the Mediterranean Basin: Origins, diffusion, and impact. Proceedings of the National Academy of Sciences of the United States of America 105:11597—11604

Zobel M, Otsus M, Liira J, Moora M, Möls T (2000) Is small-scale species richness limited by seed availability or microsite availability? Ecology 81:3274—3282

Zobel M, Partel M (2008) What determines the relationship between plant diversity and habitat productivity? Global Ecology and Biogeography 17:679 — 684

Zuloaga FO, Morrone O, Belgrano MJ (2008) Catálogo de las plantas Vasculares del Cono Sur. Website. http://www.darwin.edu.ar/Proyectos/FloraArgentina/FA.asp

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2000) Mixed effects models and extensions in ecology with R. Statistics for Biology and Health. Springer-Verlag, New York, USA

APPENDIX

Asociated with the project in which is included the present dissertation, the follow publication has been elaborated by our team:

Ovalle C, Casado MA, del Pozo A, Aravena T, de Miguel JM, Sánchez-Jardón L, Barahona V, Acosta-Gallo B, Martín-Forés I, Castro I (2015) El Espinal de la Región Mediterránea de Chile. Centro Regional de Investigación La Cruz. La Cruz, Chile. Colección libros INIA Nº 34, ISSN: 0717-4713, ISBN: 978-956-7016-46-4, 206pp

This book draws the history of origin and land-use associated with the *espinal* system and includes the flora and the fauna more representative of this cultural landscape.

“Curiosity has its own reason for existing”

Albert Einstein